National Museums
of Canada

National Museum
of Natural Sciences

Ottawa 1983

Publications in
Natural Sciences, No. 4

THE AMPHIPOD SUPERFAMILY COROPHIOIDEA IN THE NORTHEASTERN PACIFIC REGION

3. Family Isaeidae: Systematics and Distributional Ecology

K.E. Conlan
National Museum of Natural Sciences
Ottawa, Canada, K1A 0M8

Publications de
sciences naturelles, n° 4

Musées nationaux
du Canada

Musée national
de sciences naturelles

Publications in natural sciences, no. 3
Publications de sciences naturelles, n° 3
Cook, F.R. An analysis of toads of the *Bufo americanus* group in a contact zone in central northern North America.
In press

National Museum of Natural Sciences
Publications in Natural Sciences No. 4

Published by the
National Museums of Canada

© National Museums of Canada 1983

National Museum of Natural Sciences
National Museums of Canada
Ottawa, Canada

Catalogue No. NM. 95-43/4E

Printed in Canada

ISBN 0-662-11276-8
ISSN 0714-0983

Musée national des sciences naturelles
Publications de sciences naturelles n° 4

Publié par les
Musées nationaux du Canada

© Musées nationaux du Canada 1983

Musée national des sciences naturelles
Musées nationaux du Canada
Ottawa, Canada

N° de catalogue NM. 95-43/4E

Imprimé au Canada

ISBN 0-662-11276-8
ISSN 0714-0983

Contents

Abstract, v
Résumé, vi
Acknowledgements, vii
Abbreviations for figures, viii
Introduction, 1
Materials and methods, 2
Systematics section, 3
Family Isaeidae Dana, 3
Key to North Pacific Isaeidae, 3
Genus *Gammaropsis* Liljeborg, 4
Key to North Pacific species of *Gammaropsis*, 5
Gammaropsis ellisi n. sp., 6
Gammaropsis shoemakeri n. sp., 8
Gammaropsis spinosa (Shoemaker), 10
Gammaropsis thompsoni (Walker), 11
Genus *Paraeurystheus* Tzvetkova, 13
Key to North Pacific species of *Paraeurystheus*, 14
Paraeurystheus dentatus n. sp., 14
Paraeurystheus tzvetkovae n. sp., 15
Genus *Podoceropsis* Boeck, 17
Key to North Pacific species of *Podoceropsis*, 17
Podoceropsis amchitkensis n. sp., 18
Podoceropsis angustimana n. sp., 19
Podoceropsis barnardi (Kudryashov and Tzvetkova), 21
Podoceropsis chionoecetophila n. sp., 22
Podoceropsis setosa n. sp., 24
Genus *Protomedeia* Krøyer, 25
Key to species of *Protomedeia* of the North Pacific (males), 26
Key to the northeastern Pacific species of *Protomedeia* (both sexes), (Alaska to California), 26
Protomedeia articulata J.L. Barnard, 27
Protomedeia fasciata Krøyer, 28
Protomedeia grandimana Brüggen, 29
Protomedeia prudens J.L. Barnard, 31
Protomedeia stephenseni Shoemaker, 33
Genus *Cheirimedeia* J.L. Barnard, 34
Key to species of *Cheirimedeia* of the North Pacific (males), 35
Key to the northeastern Pacific species of *Cheirimedeia* (both sexes), 36
Cheirimedeia macrocarpa (Bulytscheva) *americana* n. subsp., 36
Cheirimedeia macrodactyla n. sp., 38
Cheirimedeia similicarpa n. sp., 39
Cheirimedeia zotea (J.L. Barnard), 41
Genus *Photis* Krøyer, 42
Key to species of *Photis* of the North Pacific (males), 43
Key to species of *Photis* of the North Pacific (females), 45
Photis bifurcata J.L. Barnard, 46
Photis brevipes Shoemaker, 47
Photis conchicola Alderman? 49
Photis fischmanni Gurjanova, 50
Photis lacia J.L. Barnard, 52
Photis macinerneyi n. sp., 54

Photis oligochaeta n. sp., 54
Photis pachydactyla n. sp., 56
Photis parvidons n. sp., 57
Photis cf. *spasskii* Gurjanova, 59
Genus *Chevalia* Walker, 60
Chevalia aviculae Walker, 61
Discussion and Conclusions, 63
Biogeography, 63
Distributional ecology and notes on behaviour, 63
Taxonomic considerations, 64
References, 69
Tables
1. Geographic distribution of Isaeidae collected from Alaska to northern California, 72
2. Exposure, salinity and depth range of Isaeidae collected from Alaska to northern California, 73
3. Comparison of generic level characters utilized in cluster analysis of the regional Isaeidae (Fig. 33). Plesiomorphic values are coded "O", apomorphic values are coded "1", 74

Submitted for publication: August 5, 1982
Accepted for publication: February 25, 1983

Abstract

The gammaridean family Isaeidae of the boreal and sub-Arctic eastern Pacific coast (Alaska to northern California) is examined on a taxonomic, biogeographical and ecological basis. Represented in this area are 31 species within the genera *Protomedeia* Krøyer, *Cheirimedeia* J.L. Barnard, *Gammaropsis* Liljeborg, *Paraeurystheus* Tzvetkova, *Podoceropsis* Boeck, *Photis* Krøyer, and *Chevalia* Walker. Thirteen of these species and one subspecies are new to science: *Gammaropsis ellisi*, *Gammaropsis shoemakeri*, *Paraeurystheus tzvetkovae*, *Podoceropsis amchitkensis*, *Podoceropsis angustimana*, *Podoceropsis chionoecetophila*, *Podoceropsis setosa*, *Cheirimedeia macrocarpa americana*, *Cheirimedeia macrodactyla*, *Cheirimedeia similicarpa*, *Photis macinerneyi*, *Photis oligochaeta*, *Photis pachydactyla* and *Photis parvidons*. Re-diagnosed and illustrated are, *Gammaropsis spinosa* (Shoemaker), *Gammaropsis thompsoni* (Walker), *Podoceropsis barnardi* Kudryashov and Tzvetkova, *Protomedeia articulata* J.L. Barnard, *Protomedeia fasciata* Krøyer, *Protomedeia grandimana* Brüggen, *Protomedeia prudens* J.L. Barnard, *Protomedeia stephenseni* Shoemaker, *Cheirimedeia zotea* J.L. Barnard, *Photis bifurcata* J.L. Barnard, *Photis brevipes* Shoemaker, *Photis conchicola* Alderman, *Photis fischmanni* Gurjanova, *Photis lacia* J.L. Barnard, a North American variant of *Photis spasskii* Gurjanova and *Chevalia aviculae* (Walker). In addition, *Gammaropsis dentatus* Holmes is transferred to *Paraeurystheus*, *Paraeurystheus gurvitzi* Bulytscheva is transferred to *Gammaropsis* and *Cheirimedeia* is re-diagnosed.

Phyletic relationships are developed for these and neighbouring North Pacific species through the semi-objective techniques of cluster analysis and out-group comparison of apomorphy/plesiomorphy, and *Paraeurystheus* and *Gammaropsis* are identified as the most primitive of the North Pacific genera and *Protomedeia* as considerably more apomorphic than originally thought. The dichotomous origins of the regional Isaeidae are identified, with the direction of radiation for *Gammaropsis* speculated to be northwards from the tropics, and for *Protomedeia* to be southwards from the Arctic.

Résumé

La famille, de gammaridés Isaeidae,des secteurs boréal et sub-arctique de la côte est du Pacifique (de l'Alaska au nord de la Californie) à fait l'objet d'études taxinomique, biogéographique et écologique. Sont représentées dans cette région 31 espèces appartenant aux genres *Protomedeia* Krøyer, *Cheirimedeia* J.L. Barnard, *Gammaropsis* Liljeborg, *Paraeurystheus* Tzvetkova, *Podoceropsis* Boeck, *Photis* Krøyer, and *Chevalia* Walker. Treize espèces et une sous-espèce étaient inconnues jusque-là : *Gammaropsis ellisi, Gammaropsis shoemakeri, Paraeurystheus tzvetkovae, Podoceropsis amchitkensis, Podoceropsis angustimana, Podoceropsis chionoecetophila, Podoceropsis setosa, Cheirimedeia macrocarpa americana, Cheirimedeia macrodactyla, Cheirimedeia similicarpa, Photis macinerneyi, Photis oligochaeta, Photis pachydactyla* et *Photis parvidons.* Nous avons décrit à nouveau et illustré *Gammaropsis spinosa* (Shoemaker), *Gammaropsis thompsoni* (Walker), *Podoceropsis barnardi* Kudryashov et Tzvetkova, *Protomedeia articulata* J.L. Barnard, *Protomedeia fasciata* Krøyer, *Protomedeia grandimana* Brüggen, *Protomedeia prudens* J.L. Barnard, *Protomedeia stephenseni* Shoemaker, *Cheirimedeia zotea* J.L. Barnard, *Photis bifurcata* J.L. Barnard, *Photis brevipes* Shoemaker, *Photis conchicola* Alderman, *Photis fischmanni* Gurjanova, *Photis lacia* J.L. Barnard, sous-espèce américaine du *Photis spasskii* Gurjanova et *Chevalia aviculae* (Walker). De plus, *Gammaropsis dentatus* Holmes est rattaché au genre *Paraeurystheus, Paraeurystheus gurvitzi* Bulytscheva au genre *Gammaropsis* et *Cheirimedeia* est décrit à nouveau.

On a tenté de déterminer les liens phylétiques entre les espèces précitées et les espèces voisines du nord du Pacifique au moyen des techniques semi-objectives de la taxinomie numérique et de la comparaison avec des groupes connexes pour déterminer leur apomorphie ou leur plésiomorphie. De plus, *Paraeurystheus* et *Gammaropsis* sont reconnus comme les genres les plus primitifs du nord du Pacifique et *Protomedeia* est considérablement plus apomorphique qu'on ne l'avait d'abord cru. On a déterminé la double origine des Isaeidae de la région et on a avancé l'hypothèse que *Gammaropsis* se serait dispersé vers le nord à partir des tropiques et que *Protomedeia* vers le sud à partir de l'Arctique.

Acknowledgements

The author is grateful to Dr. E.L. Bousfield of the National Museum of Natural Sciences for advisory assistance in preparation of this manuscript and plates and provision of specimens. Helpful discussions were also held with J.J. Dickinson, N.E. Jarrett, D.R. Laubitz, and W. Vader. The assistance of F.E. Zittin in preparation of the illustrations is warmly acknowledged. The author is indebted to J.L. Barnard, M.A. Bousfield, J.J. Dickinson, D.V. Ellis, P.M. Lambert, C.P. Staude, and the many other individuals and agencies cited within who provided specimens for this study.

This manuscript was prepared under contract to the National Museum of Natural Sciences, Ottawa.

ABBREVIATIONS FOR FIGURES

ABD - abdomen
GN1 - gnathopod 1
GN2 - gnathopod 2
JUV - juvenile
LFT - left
LL - lower lip
MD - mandible
MX1 - maxilla 1
MX2 - maxilla 2
MXPD - maxilliped
P5 - peraeopod 5
RT - right
U1 - uropod 1
U2 - uropod 2
U3 - uropod 3
UL - upper lip
T - telson
♂ - male
♀ - female

Introduction

The family Isaeidae comprises a diverse and possibly polyphyletic group of genera of corophioidean amphipods. Relatively few morphological characters, other than the generally glandular (silk-secreting) peraeopods 3 and 4, and fleshy telson, that are characteristic of all Corophioidea, hold constant for all members of the Isaeidae, and intergrades of several characters link the family closely to others of the superfamily. Originally conceived by Dana in 1853 to include the genera *Isaea* and *Isaeopsis*, the family Isaeidae was revised by J.L. Barnard (1969a) to encompass all members of the Photidae as well. Barnard's subsequent (1973) inclusion of the Aoridae and Isaeidae within the Corophiidae, on the basis of generic intergrades between these families, has not been generally accepted, and is not utilized herewith. In maintaining previous distinctions of component family members (e.g. Bousfield, 1979b, 1982a), Bousfield (1977) has opined that "the automatic merging of higher taxonomic units based solely on the finding of so-called "intermediate" forms . . . should be recognized as unrealistic . . . Practical lines must be drawn to preserve the usefullness and phyletic significance of the family and superfamily concept, despite exceptions to single- to few-unit characterization. The factual presence of intermediate forms lends assurance that the theory of evolution is indeed soundly based, and suggests that the Amphipoda as a crustacean group is of relatively recent origin, and is even now undergoing evolutionary "explosion"." Pertinently, Myers (1981) has maintained distinctions between families Aoridae, Corophiidae and Isaeidae, and created the new family Neomegamphopidae, in consolidating component genera, based on multiple character analysis.

The purpose of this paper is to analyze taxonomically the Isaeidae of the boreal and subarctic northeastern Pacific coastal marine region that extends southward from Alaska through British Columbia, Washington, and Oregon, to northern California at Point Conception. In assessing phyletic relationships within the regional species and genera, comparison is made with the faunas of other North Pacific regions. The North Pacific isaeid fauna has previously been documented for the western Pacific by Bulytscheva (1951, 1952), Gurjanova (1938, 1951, 1955), Kudryashov and Tzvetkova (1975), Nagata (1966), and Margulis (1963); for the coasts of Alaska by Shoemaker (1942, 1955); Oregon by J.L. Barnard (1954); and northern California by Alderman (1936), and J.L. Barnard (1959, 1962, 1966, 1969b). Virtually no systematic work on this family in the British Columbia coastal region has been accomplished to date, and very little is known of the Isaeidae of southern Alaska, Washington, and northern Oregon (see Staude, et al., 1976).

In an attempt to extend our knowledge of the marine invertebrate animals, particularly the Amphipoda, of the northeastern Pacific region, the National Museum of Natural Sciences has conducted an extensive series of collecting expeditions here since 1955 (see station lists of Bousfield, 1957, 1963, 1968; Bousfield and McAllister, 1962; and Bousfield and Jarrett, 1981). These collections provide the basis for the present study of Isaeidae, and have been extensively utilized in previous monographic accounts of the Gammaroidea (Bousfield, 1977, 1979a, b); the Talitroidea (Bousfield, 1928b, in prep.[1]; Bousfield and Hendrycks, in prep.[2]; Bousfield and Tzvetkova, in press); various families of Corophioidea (Laubitz, 1977, Conlan and Bousfield, 1982a, b, Conlan, 1982); the Ampeliscoidea (Dickinson, 1982, 1983 in press); various groups of Lysianassoidea (Jarrett and Bousfield, 1982); Atylidae (Mills, 1961) and Oedicerotoidea (Mills, 1962); and Caprellidea (Laubitz, 1977).

[1]Bousfield, E.L. (in prep.). The amphipod superfamily Talitroidea in the northeastern Pacific region: 3. Family Najnidae. Systematics and distributional ecology.

[2]Bousfield, E.L., and E. Hendrycks (in prep.). The amphipod superfamily Talitroidea in the northeastern Pacific region: 2. Family Hyalidae. Systematics and distributional ecology.

Materials and Methods

Information was compiled from the literature and from examination of several hundred thousand specimens donated or collected in National Museum survey expeditions. Station data for the National Museum survey expeditions of E.L. Bousfield for 1955 are reported in Bousfield (1958); of 1957 and 1959 in Bousfield (1963); of 1961 in Bousfield and McAllister (1962); of 1964 in Bousfield (1968); and of 1966, 1970, 1975, 1977 and 1980 in Bousfield and Jarrett (1981). Station data for other collectors are available from the National Museum of Natural Sciences, Ottawa, Canada, on request. Type specimens are deposited in the National Museum of Natural Sciences. Additional specimens of each species, where sufficient numbers allow, are deposited in the collections of the Smithsonian Institution, Washington, U.S.A., and the Zoological Institute, Leningrad, Academy of Sciences of the U.S.S.R.

Numerical analysis was by complete linkage cluster analysis using the simple matching coefficient (Sneath and Sokal, 1973). Plesiomorphy/apomorphy values were determined by outgroup comparison, utilizing the designations of J.L. Barnard (1973), Bousfield (1979) and Myers (1981). Species were awarded a value of 1 for the presence of the apomorphic form of the character and a value of 0 for the absence of this character. A value of .5 was awarded if the species was intermediate in character between the apomorphic and plesimorphic state. Keys were constructed with sex- and age-independent characters whenever possible.

Family Isaeidae Dana

Isaeidae Dana, 1853, p. 913; J.L. Barnard, 1969a, pp. 264–274, figs. 103–106; Lincoln, 1979, p. 494; Myers, 1981, p. 8; Bousfield, 1982a, p. 283.

Diagnosis

Body compressed or broad and weakly depressed; urosome segments 1 and 2 often with dorsal cusps, setae or small spines. Coxae medium to deep and overlapping, seldom separated basally; coxa 4 not excavate behind, 5 usually as deep as 4; coxae 5 and 6 anteriorly lobate. Eye small to medium, usually on anterior head lobe; inferior antennal sinus often very deep. Antennae subequal in length or antenna 2 longer; antennae elongate, slender, flagella often shorter than peduncles, frequently setose; accessory flagellum variable. Upper lip, epistome often strongly produced. Lower lip with distinct inner lobes. Mandible with strong molar and often a molar flake; lacinia mobilis with 4 teeth; palp slender, segment 3 often spatulate. Maxilla 1 inner plate with 0 to several setae. Maxilla 2, both plates well developed, inner with or without facial setae. Maxilliped plates strong, palp large but rarely segment 4 vestigial. Gnathopods moderately to strongly subchelate, 2 the larger, sexually dimorphic. Peraeopods 3 and 4, segment 2 usually not expanded. Peraeopods 5–7 not greatly dissimilar. Pleopods normal. Uropods 1 and 2 slender, uropod 1 peduncle sometimes with a posteroventral spinous process. Uropod 3 biramous or sometimes uniramous, outer ramus occasionally 2-segmented, tip not uncinate or hooked, rami as long as or longer than the peduncle. Telson entire, sometimes with dorsolateral crests. Coxal gills sac-like, on pereon segments 2–6. Brood plates large, laminar, setae simple or hook-tipped.

Component genera (other than Aoridae and Corophiidae): *Aloiloi, Ampelisciphotis (= Gaviota), Amphideutopus, Aorchoides, Audulla, Cedrophotis, Cheirimedeia, Cheiriphotis, Chevalia, Gammaropsis* (sensu lato), *Isaea, Kamaka, Kermystheus, Ledoyerella, Megamphopus, Microphotis, Microprotopus, Paradryope, Paraeurystheus, Parunciola, Photis (= Cerapopsis), Posophotis, Podoceropsis, Protomedeia, Pseudeurystheus, Segamphopus.*

Regional genera (Alaska to northern California coast): *Protomedeia, Cheirimedeia, Gammaropsis, Paraeurystheus, Podoceropsis, Chevalia, Photis.* Southern Californian and Hawaiian genera not treated but potentially occurring in this region are: *Ampelisciphotis, Amphideutopus, Cheiriphotis, Cedrophotis, Kermystheus, Megamphopus, Segamphopus.*

The Isaeidae (sens. str.) comprises about 26 world genera. Animals are small to medium in size (up to 20 mm) and occur in coastal marine and brackish waters in the intertidal or shallow subtidal, more rarely in deep water, from polar regions to the tropics of both hemispheres. Some species of *Podoceropsis* and all species of *Isaea* and *Isaeopsis* are commensal on large decapods. *Photis conchicola* inhabits small empty gastropod shells.

Key to North Pacific Isaeidae
(after J.L. Barnard, 1962, and from J.L. Barnard, 1973)

1. Uropod 3 uniramous 2
   Uropod 3 biramous 3
2. Head lobe pedunculate. Antenna 1, accessory flagellum lacking. Gnathopods 1 and 2 of both sexes similar in size ..... *Ampelisciphotis* Pirlot
   Head lobe normally acute. Antenna 1, accessory flagellum present, multisegmented. Gnathopod 2, both sexes, much larger than gnathopod 1 ..... *Cheiriphotis* Walker (in part)
3. Uropod 3 with one distinctly shortened ramus 4
   Uropod 3 with subequal rami 5
4. Antenna 1, accessory flagellum a microscopic button ..... *Photis* Krøyer (page 42)
   Antenna 1, accessory flagellum multisegmented ..... *Cheiriphotis* Walker (in part)

5. Gnathopod 1 (♂) complexly subchelate with chela projecting from segment 5. Gnathopod 2 (♂), palm well defined. Uropod 3, rami nearly twice as long as the peduncle ..... *Amphideutopus* J.L. Barnard
These characters not combined 6
6. Antenna 1, peduncular segment 3 as long as segment 1, or longer 7
Antenna 1, peduncular segment 3 shorter than segment 1 12
7. Antenna 1, accessory flagellum a microscopic button 8
Antenna 1, accessory flagellum multisegmented 9
8. Coxae deeper than wide. Upper lip with deep incision. Maxilla 1, inner plate not setose. Uropod 3, outer ramus not terminally setose ..... *Cedrophotis* J.L. Barnard
Coxae usually not deeper than wide. Upper lip not incised. Maxilla 1, inner plate setose. Uropod 3, outer ramus terminally setose ..... *Podoceropsis* Boeck[3] (page 17)
9. Antena 1, accessory flagellum composed of 3 or more segments ..... *Gammaropsis* Liljeborg (page 4)
Antenna 1, accessory flagellum composed of 1 or 2 segments 10
10. Peraeopods 5–7 with parallel edges ..... *Bonnierella* Chevreux
Peraeopods 5–7 with biconvex edges 11
11. Gnathopod 2 (♂), segment 5 at least 1.6 times as long as segment 6 ..... *Segamphopus* J.L. Barnard
Gnathopod 2 (♂), segment 5 shorter than segment 6 ..... *Megamphopus* Norman (sens. str.)
12. Urosome segments 1 and 2 coalesced ..... *Chevalia* Walker (page 60)
Urosome segments 1 and 2 separated 13
13. Peraeopods 3 and 4, dactyls short. Peraeopods 5–7, hind margin of segment 2 not setose ..... *Paraeurystheus* Tzvetkova (page 13)
Peraeopods 3 and 4, dactyls long. Peraeopods 5–7, hind margin of segment 2 setose ... 14
14. Peraeopods 3 and 4, anterior margin strongly setose (bearing more than 5 setal groups) ..... *Protomedeia* Krøyer (page 25)
Peraeopods 3 and 4, anterior margin weakly setose (bearing less than 5 setal groups) .. .. *Cheirimedeia* J.L. Barnard (page 34)

Genus *Gammaropsis* Liljeborg – J.L. Barnard, 1973

(Gammaropsis) Liljeborg, 1855, p. 455; Boeck, 1861, p. 659; 1876, p. 580; Stebbing, 1888, p. 1092; Sars, 1894, p. 557; J.L. Barnard, 1969a, pp. 264–274, pls. 103–106; 1973, pp. 17, 18; Lincoln, 1979, p. 500.
Eurystheus Bate, 1856, p. 58; 1857, p. 143; Stebbing, 1906, p. 610; J.L. Barnard, 1962, pp. 10–14.
Autonoe (part.) Bruzelius, 1859, p. 23.
Eurytheus Marschall, 1873, p. 409.
Paranaenia Chilton, 1884, p. 258.
Maeroides Walker, 1898, p. 282.
Fimbriella Stout, 1913.

Type species
Gammarus maculata Johnston, 1828 (selected by Boeck, 1876, with subsequent synonymy).

Additional species
Four regional species: *Gammaropsis shoemakeri* n. sp. (formerly *G. tenuicornis* var. *lobata* Shoemaker), *G. ellisi* n. sp., *G. spinosa* (Shoemaker), *G. thompsoni* (Walker). In addition, five species occur in the North Pacific but not regionally: *G. gurvitzi* (Bulytscheva) and *G. melanops* Sars in the U.S.S.R. and *G. tonichi* (J.L. Barnard), *G. ventosa* (J.L. Barnard) and *G. mamola* (J.L. Barnard) in southern California. Since it is possible that these species may yet be found to occur regionally, they are included for discussion. The genus, as revised by J.L. Barnard (1973), contains more than 70 species.

Diagnosis
Body not dorsoventrally depressed. Head lobe acute, antennal sinus deep. Eye medium to large, oval, lenticular or reniform. Antenna 1, peduncular segment 3 as long as segment 1, accessory

[3] Including *Kermystheus* J.L. Barnard

flagellum multisegmented; flagellum 1 longer than flagellum 2. Upper lip, epistome usually produced. Mandibular palp quite broad, segment 3 often clavate; molar with up to 6 raker spines. Maxilla 1 inner plate usually setose. Maxilla 2 bearing facial setae. Coxae often short, lower margins not setose, not shallowing posteriorly. Coxa 1 not produced forward; coxae 1 and 2 (♂) usually not shallower than coxae 3-5; coxa 3 (♂) lacking stridulation ridges. Gnathopod 1, segment 5 not produced into a posterior lobe; palm and dactyl variable. Gnathopod 2 (♂), segment 2 lacking stridulation ridges; segment 5 usually shorter than segment 6, length of posterior margin variable; palm not incised. Peraeopods 3 and 4, length of segment 4 variable; dactyl short. Peraeopod 5 (♂), segment 2 not posterodistally notched; segment 4 normal; dactyl lacking an accessory tooth. Peraeopods 6 and 7 similar in form to but generally longer than peraeopod 5; segment 2, hind margin not setose; segment 5 bearing comb spines. Pleopods normal. Epimera 1-3 sometimes posterodistally notched and bearing a lateral ridge, this occurring in conjunction with dorsal cusping of the urosome. Uropod 1 bearing a peduncular spinous process; uropods 1 and 2 terminating in a group of spines. Uropod 3 ordinary or with peduncle elongate; outer ramus one-segmented, terminating in spines or setae (outer ramus two-segmented in some Hawaiian species (Barnard, 1970), but not in regional species); inner ramus half or more the length of the outer. Telson bearing a pair of small apical cusps or strong spines. Brood plates medium, oval or leaf-shaped; setae dense, hook-tipped.

Distribution

Cosmopolitan, mostly littoral, with a few deep water forms (Lincoln, 1979).

Remarks

Barnard (1973) appended to *Gammaropsis* the genera *Audulla*, Chevreux, *Bonnierella* Chevreux, *Kermystheus* J.L. Barnard, *Megamphopus* Norman, *Podoceropsis* Boeck, *Pseudeurystheus* Schellenberg, *Segamphopus* J.L. Barnard and an unnamed subdivision. Each was found to intergrade or be characterized by apparently insignificant anomalies, indicating strong polyphyletally. However, for the purposes of this report and for reasons advanced subsequently (see Discussion and Conclusions), the regional *Gammaropsis, Podoceropsis* and *Paraeurystheus* are treated as distinct genera. Southern genera that are presently unknown for, but could penetrate the study region, are *Bonnierella* Chevreux, *Kermystheus* J.L. Barnard and *Megamphopus* Norman.

The North Pacific species of *Gammaropsis* are subdivisible by morphology and geography into two groups which on further analysis and comparison with other world species may warrant taxonomic status. One group, comprising all northern boreal species, is more closely related to *Paraeurystheus*, while the other, a southern boreal group, shows closer afinities to the Atlantic type *G. maculata* and to *Podoceropsis*. Regional representatives of the northern boreal group are *G. shoemakeri* n. sp., *G. ellisi* n. sp., and *G. thompsoni* (Walker); of the southern boreal group is *G. spinosa* (Shoemaker).

Key to North Pacific Species of Gammaropsis

1. Urosome dorsally cusped. Peraeopods 3 and 4, segments 4 and 5 subequal 2
   Urosome not dorsally cusped. Peraeopods 3 and 4, segment 4 half to three-quarters the length of segment 5 6
2. Head lobe shallow, rounded. Eye small, oval. Uropod 3, outer ramus shorter than the inner ..... *Gammaropsis gurvitzi* (Bulytscheva, 1952)
   Head lobe produced, acute. Eye large, reniform. Uropod 3, rami subequal 3
3. Head lobe not distally toothed. Gnathopods 1 and 2 (♂), margins of segment 2 not setose. Gnathopod 2 (♀), palm excavate. Coxa 7 (♂) not expanded. Urosome segments 1 and 2, carinations rounded ..... *Gammaropsis ellisi* n. sp. (page 6, fig. 1)
   Head lobe distally toothed. Gnathopods 1 and 2 (♂), margins densely setose. Gnathopod 2 (♀), palm not excavate. Coxa 7 (♂) expanded. Urosome segments 1 and 2, carinations pointed 4

4. Gnathopod 1 (♂), segment 2 anterodistally produced into a lobe. Gnathopod 2 (♂, ♀), palm lacking a tooth; coxa 7 (♂) slightly expanded ..... *Gammaropsis shoemakeri* n. sp. (page 8, fig. 2)
   Gnathopod 1 (♂), segment 2 not anterodistally produced into a lobe; gnathopod 2 (♂, ♀), palm bearing a tooth; coxa 7 (♂) greatly expanded 5
5. Gnathopod 2 (♂), palm nearly transverse, bearing both a medial tooth and a defining tooth ..... *Gammaropsis thompsoni* (Walker, 1898) (page 11, fig. 4)
   Gnathopod 2 (♂), palm oblique, bearing a medial tooth but no defining tooth ..... *Gammaropsis tonichi* J.L. Barnard, 1962
6. Gnathopod 2 (♂) much heavier than gnathopod 1, segment 5 much shorter than segment 6 and posteriorly lobate. Uropods 1 and 2, longest ramus shorter than the peduncle. Uropod 2 bearing a peduncular spinous process. Uropod 3, outer ramus medially setose ..... *Gammaropsis ventosa* (J.L. Barnard, 1962)
   Gnathopod 2 (♂) not greatly heavier than gnathopod 1, segment 5 at least as long as segment 6, posterior margin more than half the length of the anterior margin and not lobate. Uropods 1 and 2, rami subequal or longer than the peduncle. Uropod 2 lacking a peduncular spinous process. Uropod 3, outer ramus only terminally setose 7
7. Coxae 1–5 deeper than the body plates. Gnathopod 2 (♀), palm excavate. Peraeopods 3 and 4, segment 4 produced over segment 5. Peraeopod 5 (♂), segment 2 much wider than segment 2 of peraeopods 6 and 7, segment 4 expanded, hind margin spinose. Epimera 1–3, posterodistal corner not notched ..... *Gammaropsis spinosa* (Shoemaker, 1942)(page 10, fig. 3)
   Coxae 1–5 not deeper than the body plates. Gnathopod 2 (♀), palm not excavate. Peraeopods 3 and 4, segment 4 not produced over segment 5. Peraeopod 5 (♂), segment 2 not much wider than segment 2 of peraeopods 6 and 7, segment 4 not expanded, hind margin not spinose. Epimera 1–3, posterodistal corner notched 8
8. Eye reniform. Head lobe produced into a tooth. Gnathopod 2 (♀), palm bearing a tooth. Uropod 3, rami as long as the peduncle ..... *Gammaropsis melanops* (Sars, 1885)
   Eye lenticular. Head lobe not produced into a tooth. Gnathopod 2 (♀), palm lacking a tooth. Uropod 3, rami longer than the peduncle ... *Gammaropsis mamola* (J.L. Barnard, 1962)

Gammaropsis ellisi n. sp.
Figure 1

Material examined

Holotype, ♂ – Nahwitti Bar, entrance to Goletas Channel, B.C. (50°55′N, 128°02′W). Bousfield 1959 stn. V3, 6–10 fm dredge on sand, stones and shell. 17 July 1959. Allotype, ♀ paratype – off Edward King Island, Barkley Sound, Vancouver Island, B.C. (48°49.08′N, 125°12.05′W). Collected from a sponge by W.C. Austin, 7 July 1976. Holotype, ♂, NMC-C-1981-918; allotype, ♀, NMC-C-1981-920; paratype, 1 immature NMC-C-1981-919.

Additional material

Alaska – southern tip: 1 specimen from Bousfield and McAllister stn. A3 (Little Daykoo, Dall Island).

British Columbia – Queen Charlotte Islands: 16 specimens from Bousfield 1957 stns. E14a and W4b. Northern mainland: 13 specimens from Bousfield 1964 stns. H12, H50, H65 (1 ♂, 3 ♀ ♀, 5 immatures deposited in the Leningrad Museum). Vancouver Island: 3 specimens from Bousfield 1977 stn. B6a; 2 specimens from Bousfield 1976 stn. B25; 7 specimens from Bousfield 1975 stns. P17d, P29a (5 ♂♂, 1 ♀ deposited in the Smithsonian Institution (USNM)); 35 specimens from Bousfield 1970 stns. P710, P712, P713, P714; 8 specimens from Bousfield 1959 stn. V3; 7 specimens from the collections of W.C. Austin, D.B. Quayle and the B.C. Provincial Museum.

Diagnosis

Holotype, male, 7.0 mm: Eye reniform; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxa 1 not markedly shallower than coxa 2; coxae 1–5 nearly as deep as the body plates coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm oblique. Gnathopod 2, segment 2 not setose; seg-

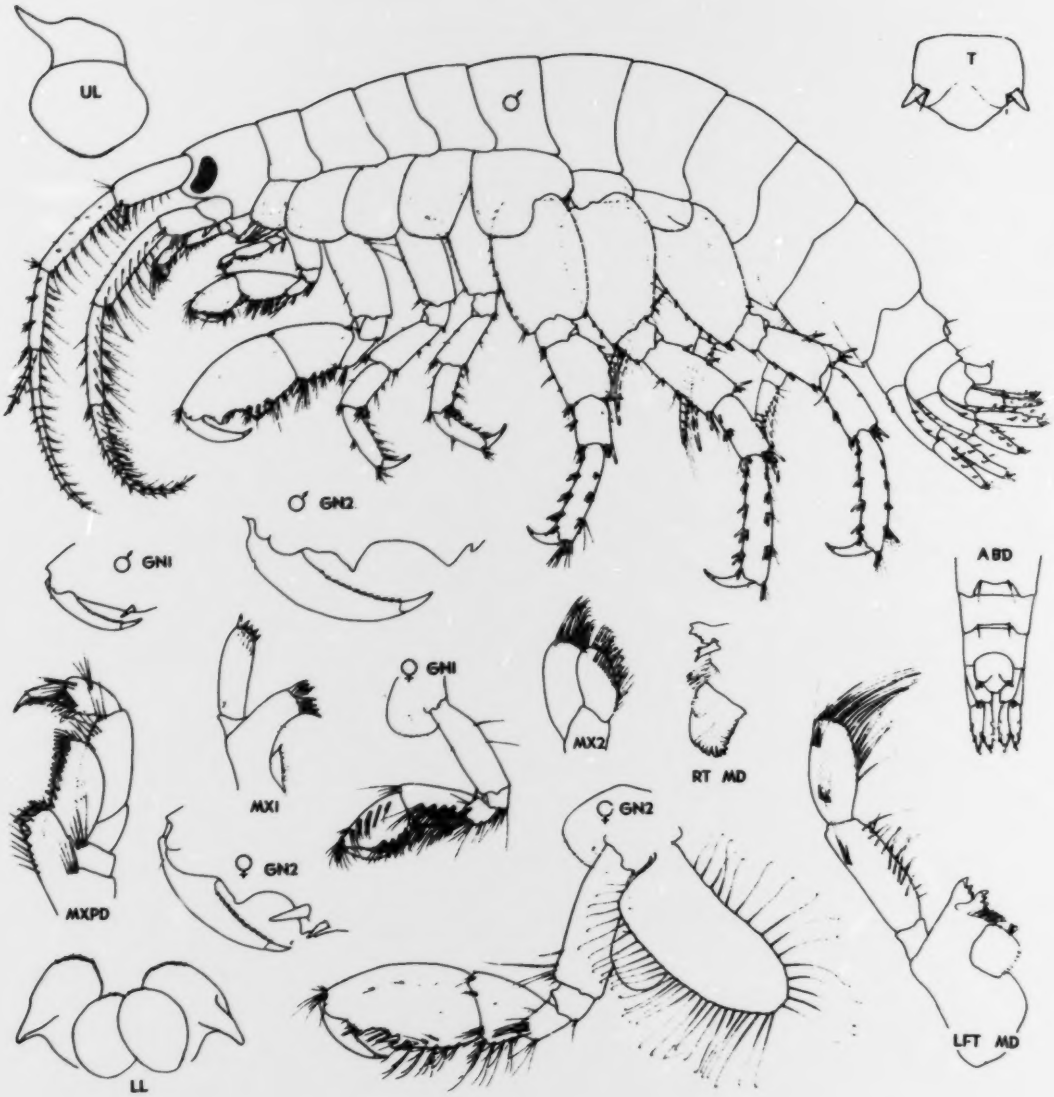


Figure 1. *Gammaropsis ellisi* n. sp. ♂ 7.0 mm, Nahwitti Bar, B.C.; ♀ 8.0 mm, Edward King Is., Barkley Sound, Vancouver Is., B.C.

ment 5 shorter than segment 6, posterior margin more than half the length of the anterior margin and not produced into a lobe; segment 6, palm bearing a process and defined only by a change of angle; dactyl not longer than the palm. Peraeopods 3 and 4, segment 4 not overhanging and barely longer than segment 5. Peraeopod 5, segment 2 not posterodistally notched and hardly wider than segment 2 of peraeopods 6 and 7; segment 4 expanded, hind margin spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin spinose. Urosome, segments 1 and 2 bearing a rounded tooth and a seta on either side of a broad truncate lobe. Epimera 1–3 bearing a lateral ridge, posterodistal corner strongly notched. Uropod 1, peduncular spinous process half the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal, neither setose. Telson terminating in a small seta and a strong spine at each apex.

Allotype, female, 8.0 mm: Gnathopod 2, segment 5 much shorter than segment 6, posterior margin half the length of the anterior margin but not produced into a lobe; segment 6, palm defined by a sharp change of angle and two spines. Other features similar to the male.

Size range: male to 7.0 mm, female 4.5 to 8.0 mm.

Distribution

Dall Island, southeastern Alaska (54°42′N, 132°42′W) south to Trial Island, Vancouver Island, B.C. (48°23′N, 123°18′W).

Ecology

Occurs on high salinity exposed and semi-protected coasts amongst sponges and algae on coarse substrates at low water level to 72 m depth. Summer temperature ranges documented in the collections of Bousfield, 1959 to 1977, were 10–14.5°C, salinity 30.0 to 33 + °/oo.

Life history

Females ovigerous July to August.

Remarks

This species most closely resembles *G. gurvitzi* (Bulytscheva 1952) (formerly *Paraeurystheus*) but differs in the shape of the head lobe and eye, the male and female second gnathopod, and the male peraeopod 5, and in the form of uropod 3.

Etymology

This species is named after Dr. D.V. Ellis, University of Victoria, B.C., in recognition of his many contributions to Pacific invertebrate taxonomy.

Gammaropsis shoemakeri n. sp.
Figure 2

Eurystheus tenuicornis var. *lobata* Shoemaker, 1942, pp. 28–29, fig. 10a–c.

Material examined

Holotype, ♂, allotype, ♀, paratypes – Hesquiat, at Matlakaw Point, Vancouver Island, B.C. (49°11′N, 126°01′W). Bousfield 1959 stn. O11, low water level, boulders, gravel, shale, kelp, *Phyllospadix*; temperature 14.5°C, salinity 31.2°/oo. 19 August 1959. Holotype, ♂, NMC-C-1982-100; allotype, ♀, NMC-C-1982-101; paratypes, 3♂♂, 5♀♀, 3 immatures NMC-C-1982-102.

Additional material

British Columbia – Vancouver Island: 3 specimens from Bousfield 1955 stn. P7, protected bay just north of Quisitis Point; gravel beach interspersed with rocks and boulders, dense kelp beds; collection at low water level; temperature 12.2°C, salinity 31.2 °/oo.

Washington: 1 specimen from Bousfield 1966 stn. W40, Mukkaw Bay at Sooes Point, Clallam County; fine sand, shelly sand, soft sandstone, bedrock and boulders; kelp, *Phyllospadix, Zostera* and *Chorda*; collection at low water to mean water levels; temperature 12.3°C; salinity 32.6 °/oo.

Diagnosis

Holotype, male, 5.5 mm: Eye reniform; head lobe acute and distally toothed. Antenna 1, peduncular segment 1 bearing 2 thin posterodistal spines. Upper lip, epistome produced. Coa 1 not shallower than coxa 2; coxae 1–5 shallower than the body plates; coxa 7 moderately expanded. Gnathopod 1, segment 2 strongly setose and produced into a posterodistal lobe; segment 6, palm broadly oblique. Gnathopod 2, segment 2 strongly setose; segment 5 shorter than segment 6, posterior margin half the length of the anterior margin and not produced into a lobe; segment 6, palm oblique, lacking a medial process and not defined; dactyl not longer than the palm. Peraeopods 3 and 4, segment 4 not overhanging and subequal to segment 5. Pareopod 5, segment 2 not posterodistally notched and not wider than segment 2 of peraeopods 6 and 7; segment 4 not expanded, hind

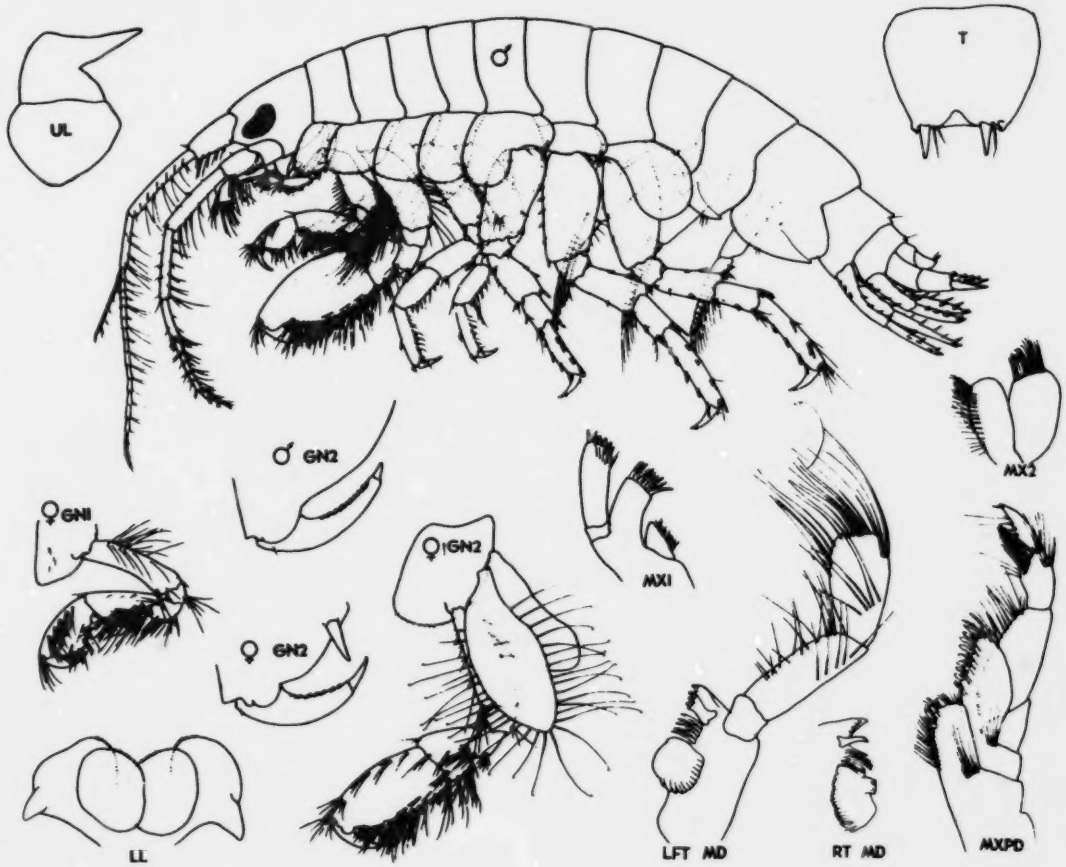


Figure 2. *Gammaropsis shoemakeri* n. sp. ♂ 5.5 mm, ♀ 5.5 mm. Hesquiat, Vancouver Is., B.C.

margin spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin spinose. Urosome, segments 1 and 2 bearing dorsally a sharp tooth and a seta on either side of a broad truncate lobe. Epimera 1–3 bearing a lateral ridge, posterodistal corner strongly notched. Uropod 1, peduncular spinous process nearly half the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal, neither setose. Telson terminating in one or two setae and a spine on either corner.

Allotype, female, 5.5 mm: coxa 1 not shallower than coxa 2, Gnathopod 2, segment 2 moderately setose and not posterodistally lobed; segment 5 shorter than segment 6, posterior margin more than half the length of the anterior margin and not produced into a lobe; segment 6, palm oblique, defined by a strong spine, but lacking a medial tooth. Coxa 7 not expanded. Other features similar to the male.

Juvenile male: similar to the female.
Size range: male to 5.5 mm, female 4 to 5.5 mm.

Distribution

Hesquiat, Vancouver Island, B.C. (49°11′N, 126°01′W) south to Magdalena Bay, Baja, California (26°42′30″N, 113°34′15″W).

Ecology

Occurs amongst algae and hybroids on high salinity, exposed and semi-protected coasts at low water level, to 27 m depth.

Remarks

Although Shoemaker (1942) originally termed this species a variant of *Gammaropsis thompsoni* (i.e. *Eurystheus tenuicornis* van *lobata*, specimens differ considerably more from the nominate species than does the more similar but distinctly

designated species *G. tonichi* J.L. Barnard, 1962. Notable differences occur in the form of the male gnathopods 1 and 2, shape and size of coxa 7, size at maturity and geographic distribution. Distinction at the species level is therefore warranted. This species is distinct from *Gammaropsis lobatus* Chevreux and Fage, 1925.

Etymology

The *lobata* variety name given by Shoemaker (1942) has no taxonomic significance and, on a specific scale, has been pre-empted by Chevreux and Fage (1925). This species is therefore named after C.R. Shoemaker in recognition of his contribution.

Gammaropsis spinosa (Shoemaker)
Figure 3

Eurystheus spinosus Shoemaker, 1942, pp. 30–32, fig. 11; J.L. Barnard, 1969b, pp. 142–146, fig. 31.

Material examined

British Columbia — Vancouver Island: 2 specimens from Bousfield 1975 stn. P29a, Gooding Cove, entrance to Quatsino Sound, 16 August 1975; gravel, coarse sand, algae; 20 m dredge, 11°C, 33+ °/oo; 2 specimens from Bousfield 1970 stn. P710, Cape Beale, 19 July 1970; bedrock, sand; low water level, 13.3°C.

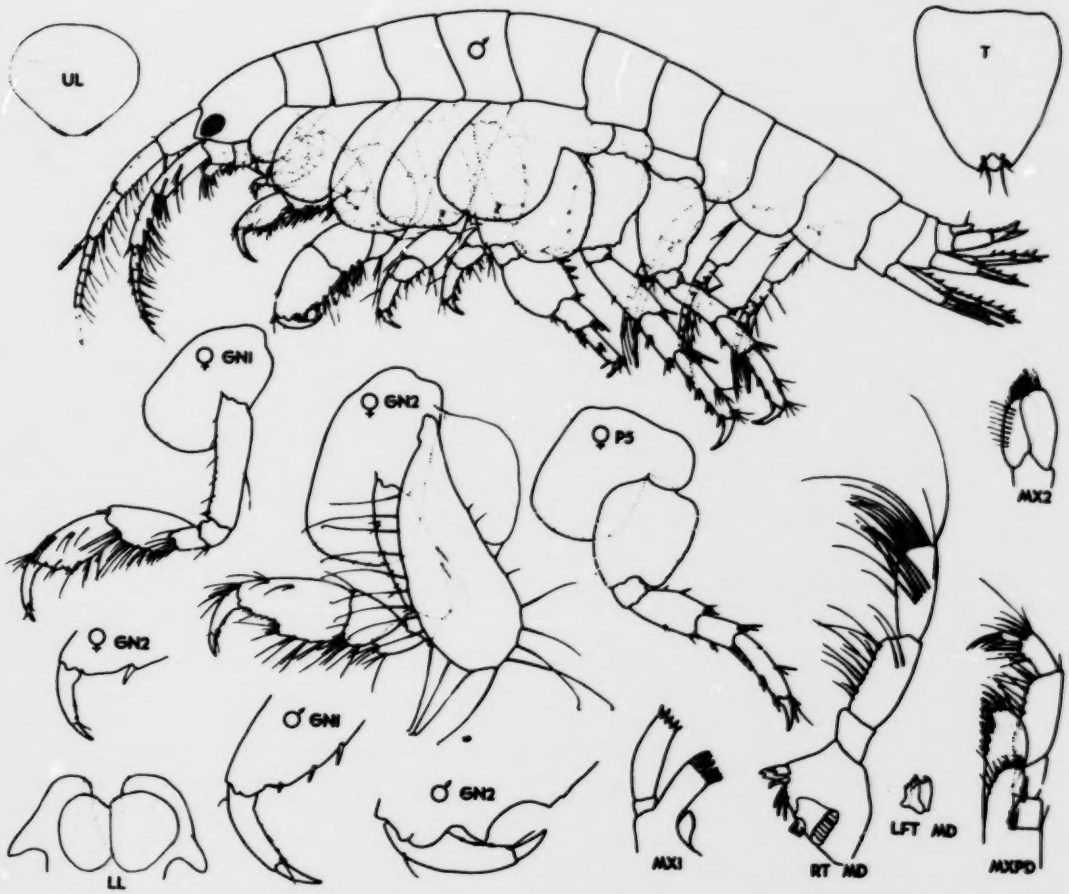


Figure 3. *Gammaropsis spinosa* (Shoemaker) ♂ 3.0 mm, Gooding Cove, Quatsino Sound, Vancouver Is., B.C.; ♀ 3.0 mm, Cape Beale, Barkley Sound, Vancouver Is., B.C.

Diagnosis

Male: Eye lenticular; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 lacking a posterodistal spine. Upper lip, epistome not produced. Coxa 1 markedly shallower than coxa 2; coxae 1–5 deeper than the body plates; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm slender, very oblique. Gnathopod 2, segment 2 not setose; segment 5 subequal to segment 6, posterior margin more than half the length of the anterior margin and not produced into a lobe; segment 6, palm bearing a medial process and defined by a sharp change of angle; dactyl not longer than the palm. Peraeopods 3 and 4, segment 4 overhanging and longer than segment 5. Peraeopod 5, segment 2 not posterodistally notched and much wider than segment 2 of peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 4, posterior margin not spinose. Urosome, segments lacking dorsal setae or cusps. Epimera lacking a lateral ridge, posterodistal corner not notched. Uropod 1, peduncular spinous process half the length of the longest ramus. Uropod 2, peduncular process lacking Uropod 3, outer ramus slightly shorter than the inner; outer ramus neither medially nor terminally setose. Telson terminating in one or two setae and cusp at each distal corner.

Female: Coxa 1 markedly shallower than coxa 2. Gnathopod 2, segment 5 shorter than segment 6, posterior margin about two thirds the length of the anterior margin and not produced into a lobe; segment 6, palm lacking a medial tooth, but defined by a spine. Peraeopod 5, segments 2 and 4 less expanded, segments 5 and 6 longer; other features similar to the male.

Size range: male to 3.0 mm, female 3.0 to 3.5 mm.

Distribution

Quatsino Sound, Vancouver Island, B.C. (50°24′N, 127°57′W) south to Magdalena Bay, Baja California (26°42′30″N, 113°34′15″W).

Ecology

An exposed coast, high salinity species found amongst algae, sponges and soft polychaete tubes on gravel and sand at low water level to 27 m depth.

Life history

Females ovigerous in July.

Remarks

This species bears many features that are uncommon to other Pacific species of *Gammaropsis*, viz. the unproduced upper lip, the deep coxal plates, the slenderer first gnathopod palm, the *Podoceropsis*-like peraeopods 3 and 4, the urosome lacking setation and the very small body size.

Gammaropsis thompsoni (Walker) (Barnard, 1959)

Figure 4

Maeroides thompsoni Walker, 1898, pp. 283–384, pl. 16, figs. 3–6.
Gammaropsis tenuicornis Holmes, 1904, pp. 239–240, fig. 124.
Fimbriella robusta Stout, 1913, pp. 642–644.
Podoceropsis concava Shoemaker, 1916, pp. 159–160.
Eurystheus tenuicornis Shoemaker, 1931, pp. 5–8, figs. 3, 4; Alderman, 1936, p. 67; Shoemaker, 1941, p. 185; Shoemaker, 1942, p. 28, fig. 10; Hewatt, 1946, pp. 199, 204.
Eurystheus thompsoni (Walker, 1898): Shoemaker, 1955, p. 59; J.L. Barnard, 1959, p. 36, pl. 11; 1961, p. 182; 1966, p. 62; 1969b, p. 146.

Material examined

Alaska — 2 specimens from Bousfield 1980 stns. S4B1 and S18F3; 1 specimen from Bousfield and McAllister stn. A3.

British Columbia — Queen Charlotte Islands: 19 specimens from Bousfield 1957 stns. H8b, H14 and W4b. Northern mainland: 143 specimens from Bousfield 1964 stns. H1, H5, H12, H21, H22, H23, H33, H47, H49, H50, H52, H53, H57 and 4 specimens from the collection of J.W. Scoggan. Vancouver Island and southern mainland: 301 specimens from Bousfield 1977 stns. B6a, B8, B11b, B12a, B13 (3♂♂, 6♀♀ deposited in the Smithsonian Institution (USNM)), B14, B17, B18, B21a, B21b (13♂♂, 16 ♀♀, 8 immatures deposited in the Zoological Institute, Leningrad; 197 specimens from Bousfield 1976 stns. B4, B5, B7, B9a, B9d, B10a, B10c, B10d, B17, B25, B27, B28; 222 specimens from Bousfield 1975 stns. P5a, P9, P11, P12, P13, P14a, P17a, P17d, P20, P21a, P21b, P29a, P29b, P29c; 81 specimens from Bousfield 1970 stns. P702, P710, P711, P712,

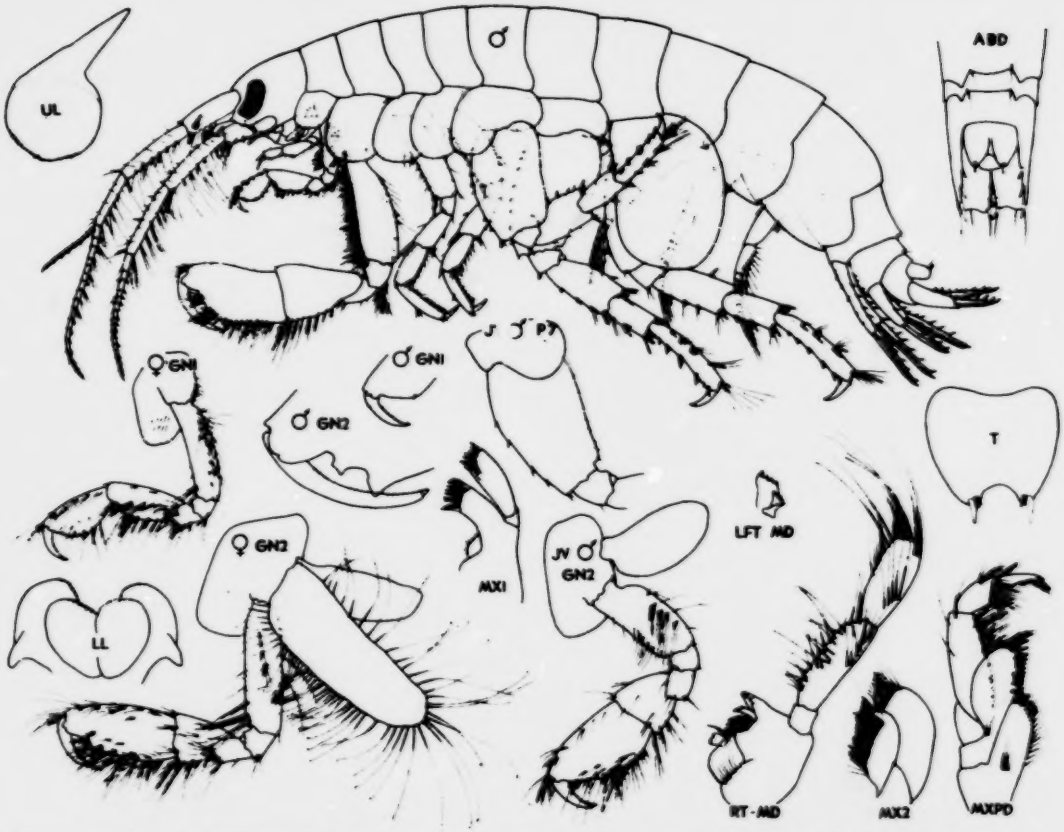


Figure 4. *Gammaropsis thompsoni* (Walker) ♂ 10.0 mm, jv ♂ 4.5 mm, ♀ 8.5 mm, Cape Beale, Barkley Sound, Vancouver Is., B.C.

P714, P715, P718, P719; 61 specimens from Bousfield 1959 stns. V3, O1, O3, O5, O6, O7b, O7d, O12, O13; 52 specimens from Bousfield 1955 stns. F3, P2, P7; and 24 specimens from the collections of K.E. Conlan, L. Daniels, D.V. Ellis, G. O'Connell and D.B. Quayle.

Washington — 23 specimens from Bousfield 1966 stns. W30, W35, W40.

Diagnosis

Male: eye reniform; head lobe acute and distally toothed. Antenna 1, peduncular segment 1 bearing two thin posterodistal spines. Upper lip, epistome produced. Coxa 1 markedly shallower than coxa 2; coxae 2–5 slightly shallower than the body plates; coxa 7 greatly expanded (less so in the juvenile). Gnathopod 1, segment 2 strongly setose but not produced into a posterodistal lobe; segment 6, palm broadly oblique. Gnathopod 2, segment 2 strongly setose; segment 5 subequal to segment 6, posterior margin more than half the length of the anterior margin and not produced into a lobe; segment 6, palm transverse, bearing a medial process and defined by a tooth; dactyl longer than the palm. Peraeopods 3 and 4, segment 4 not overhanging, and subequal to segment 5. Peraeopod 5, segment 2 not posterodistally notched and not wider than segment 2 of peraeopods 6 and 7; segment 4 hardly expanded, hind margin spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin spinose. Urosome, segments 1 and 2 bearing dorsally a sharp tooth and seta on either side of a broad truncate lobe. Epimera 1–3 bearing a lateral ridge, posterodistal corner strongly notched. Uropod 1, peduncular spinous process a third the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal; outer ramus neither medially nor terminally setose. Telson terminating in a few seta and a spine on either corner.

Female: coxa 1 only slightly shallower than coxa 2. Gnathopod 2, segment 2 weakly setose; segment 5 shorter than segment 6, posterior margin more than half the length of the anterior margin and not produced into a lobe; segment 6, palm oblique, undefined and bearing a small medial tooth. Coxa 7 not expanded. Other features similar to the male.
Juvenile male: similar to the female, but palm of gnathopod 2 lacking a tooth and defined by a spine.
Size range: male to 11.5 mm, female 4.5 to 10.0 mm.

Distribution
Southeastern Alaska (57°29′N, 135°58′W) south to the San Diego shelf of southern California (33°N, 118°W).

Ecology
Abundant amongst kelp holdfasts, rarer amongst *Phyllospadix*, tunicates, sponges and worm tubes. A high salinity exposed or semi-protected coastal species occurring on sandy sediments, at low water to a depth of 72 m. Summer temperature ranges documented in the collections of Bousfield, 1955 to 1980, were 10–14.2°C, salinity 28.0–33+ °/oo

Life history
Females ovigerous in May to August.

Remarks
Examination of colour photographs of live specimens shows a distinctive orange and white banding of the antennae and brown and white banding of the body segments and coxae.

Genus *Paraeurystheus* Tzvetkova
Paraeurystheus Tzvetkova, 1977, pp. 88–101, figs. 1–4.

Additional species
There are six species in this genus known worldwide. *P. anamae* Gurjanova, *P. gurjanovae* Tzvetkova, *P. latipes* Tzvetkova, and *P. sexdentatus* (Stephensen) occur in the U.S.S.R., while *P. dentatus* (Holmes) (formerly *Eurystheus dentatus*) and *P. tzvetkovae* n. sp. occur in the Bering Sea. A seventh species named by Tzvetkova (1977), *Paraeurystheus gurvitzi*, is more appropriately placed within the genus *Gammaropsis* (see Discussion).

Diagnosis
Body not dorsoventrally depressed. Head lobe not acute, antennal sinus shallow. Eye circular, reniform or oval. Antenna 1, peduncular segment 3 shorter than segment 1, accessory flagellum multisegmented; flagellum 1 longer than flagellum 2. Upper lip, epistome produced. Mandibular palp quite broad, segment 3 clavate; molar with up to 6 raker spines. Maxilla 1 inner plate setose, but lacking a single long terminal seta. Maxilla 2 bearing facial setae. Coxae short, lower margins not setose, not shallowing posteriorly. Coxa 1 produced forward; coxae 1 and 2 (♂) not shallower than coxae 3–5; coxa 3 (♂) lacking stridulation ridges. Gnathopod 1, segment 5 not produced into a posterior lobe; segment 6 broad, palm oblique, dactyl not extending far beyond the palm. Gnathopod 2 (♂), segment 2 lacking stridulation ridges; segment 5 much shorter than segment 6, often greatly narrowed posteriorly and sometimes lobed; palm not incised. Peraeopods 3 and 4, segment 4 hardly longer than segment 5 and not anterodistally produced; dactyl short. Peraeopod 5 (♂), segment 5 not posterodistally notched; segment 4 normal; dactyl lacking an accessory tooth. Peraeopods 6 and 7 (♂) and sometimes 5 often greatly expanded; segment 2, hind margin not setose, segment 5 bearing comb spines. Pleopods normal. Epimera 1–3 strongly notched posteriorly and bearing a lateral ridge, this occurring in conjunction with dorsal cusping of the urosome. Uropod 1 bearing a peduncular spinous process; uropods 1 and 2 terminating in a group of spines. Uropod 3, rami often unequal, terminally setose. Telson bearing a pair of small apical cusps. Brood plates unknown, probably similar to those of *Gammaropsis*.

Distribution
A cold water group occurring on the northern east and west coasts of the Pacific.

Remarks
Tzvetkova (1977) defines this group as a distinctive genus, differing from *Gammaropsis* in the form of antenna 1, gnathopod 2 (♂), peraeopods 5–7 and uropod 3. However, in other features which are deemed diagnostic, such as the form of the mandibular palp, gnathopod 1 and the urosome, there is no apparent difference from *Gammaropsis*.

Key to North Pacific Species of Paraeurystheus

1. Uropod 3, inner ramus half the length of the outer ramus 2
   Uropod 3, inner ramus more than half the length of the outer ramus 3
2. Uropod 3, inner ramus terminally setose. Gnathopod 2(♂) enlarged, palm transverse and bearing a tooth. Peraeopods 6 and 7 (♂) enlarged, segments 4 and 5 expanded. ... . *Paraeurystheus tzvetkovae* n. sp. (page 15, fig. 6)
   Uropod 3, inner ramus not setose. Gnathopod 2 (♂) similar to and not greatly larger than gnathopod 1. Peraeopods 6 and 7 (♂) not enlarged, segments 4 and 5 not expanded ..... *Paraeurystheus dentatus* (Holmes, 1980) (page 14, fig. 5)
3. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Coxa 1 (♂) not markedly shallower than coxa 2. Uropod 1, peduncular spinous process more than half the length of the longest ramus 4
   Antenna 1, peduncular segment 1 lacking a posterodistal spine. Coxa 1 (♂) shallower than coxa 2. Uropod 1, peduncular spinous process less than half the length of the longest ramus 5
4. Eye round. Coxae 3 and 4 not shallower than the body plates. Peraeopods 6 and 7 (♂), segments 2, 4, 5 greatly expanded. Uropod 3, rami as long as the peduncle..... ..... *Paraeurystheus anamae* Gurjanova, 1952
   Eye reniform. Coxae 3 and 4 much shallower than the body plates. Peraeopods 6 and 7 (♂), segments 2, 4, 5 not expanded. Uropod 3, rami much longer than the peduncle . ..... *Paraeurystheus gurjanovae* Tzvetkova, 1977
5. Eye reniform. Head lobe acute. Peraeopod 7 (♂), segments 2 and 4 expanded .... *Paraeurystheus latipes* Tzvetkova, 1977
   Eye oval. Head lobe rounded. Peraeopod 7 (♂), segments 2 and 4 not expanded .... *Paraeurystheus sexdentatus* (Stephensen, 1944)

Paraeurystheus dentatus (Holmes)
Figure 5

Eurystheus dentatus Holmes 1908, p. 541, fig. 46; not Gurjanova, 1938, p. 341, fig. 44, not Gurjanova, 1951, p. 853, fig. 598.

Material examined
1 subadult ♂, 10.0 mm, from Kalikta Beach, Unalaska Island, Alaska at 3.6 m depth; N.A. Powell, collector.

Diagnosis
Male: eye oval to rectangular; head lobe shallow, flattened and not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxa 1 anteriorly produced, not markedly shallower than coxa 2; coxae 1–5 shallower than the body plates; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm broadly oblique. Gnathopod 2, segment 2 not setose; segment 5 shorter than segment 6, posterior margin half the length of the anterior margin and broadly lobate; segment 6, palm lacking a process and defined by a spine; dactyl not extending beyond the palm. Peraeopods 3 and 4, segment 4 not overhanging and hardly longer than segment 5. Peraeopod 5, segment 2 not posterodistally notched, and wider than segment 2 of peraeopods 6 and 7; segment 4 not expanded, hind margin not spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin not spinose. Urosome, segments 1–3 bearing dorsally a pair of setae and strong cusp. Epimera 1–3 bearing a lateral ridge, posterodistal corner strongly notched. Uropod 1, peduncular spinous process two thirds the length of the longest ramus. Uropod 2, peduncular process present. Uropod 3, inner ramus half the length of the outer, not terminally setose; outer ramus both medially and terminally setose. Telson terminating in two clusters of setae and a pair of small cusps.
Female: coxa 1 anteriorly produced, not markedly shallower than coxa 2. Other features similar to the male.
Size range: male to 12.0 mm, female to 11.0 mm.

Distribution
Aleutian Islands, Alaska: Afognak Island and Unalaska Island (53°N, 166°W).

Ecology
An Arctic species occurring at 3.6 m to 90 m depth.

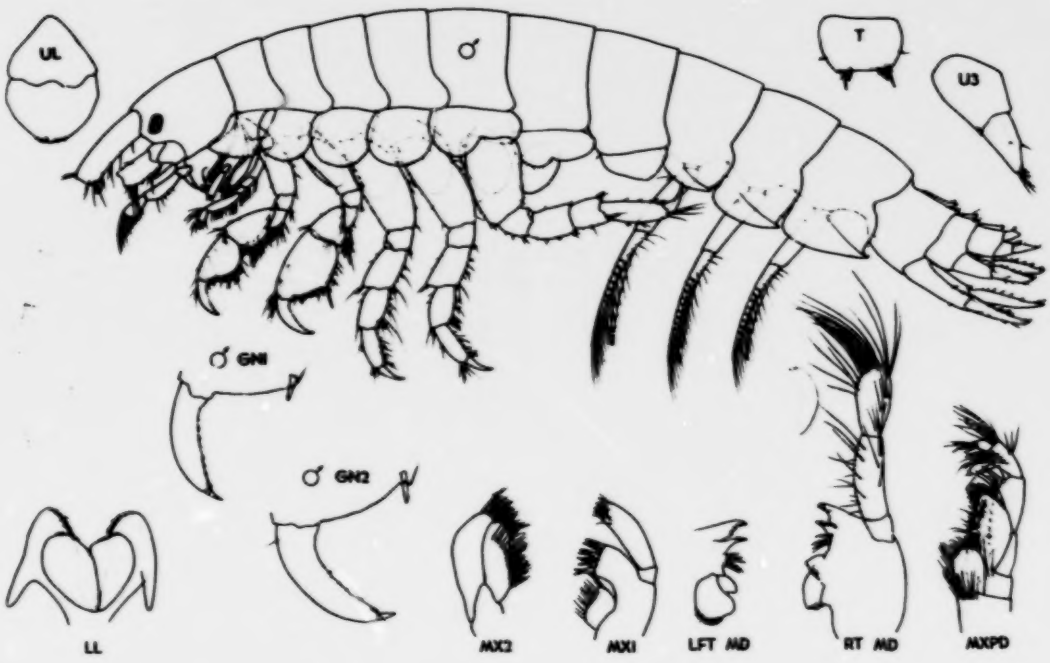


Figure 5. *Paraeurystheus dentatus* (Holmes) ♂ 10.0 mm, Unalaska Is., Alaska.

Remarks

This specimen lacked peraeopods 6 and 7 and antennae 1 and 2. However the form of the head lobe, small undifferentiated second gnathopod, toothed dorsum, long uropod peduncular spinous processes and the short, non-setose inner ramus of uropod 3 are distinctive. Gurjanova's 1938 and 1951 specimens were transferred to a new species, *Paraeurystheus gurjanovae* by Tzvetkova (1977). *P. dentatus* differs from *P. gurjanovae* in an unaltered ♂ gnathopod 2, longer peduncular spinous process of uropod 1, and uropod 3 rami shorter than the peduncle with the inner no more than half the length of the outer. However this species retains many other characters in common with *Paraeurystheus*, viz. a shallow head lobe, shortened segment 3 of antenna 1, anteriorly produced coxa 1, posteriorly narrowed segment 5 of gnathopod 2 and terminally setose uropod 3. It is, therefore, more appropriately placed in this genus.

Paraeurystheus tzvetkovae n. sp.
Figure 6

Material examined

Constantine Harbour, Amchitka Island, Aleutian Islands, Alaska (52°N, 179°W). 1♂. P. Slattery collection, 24 April 1969.
Holotype, ♂, (NMC-C-1982-61).

Diagnosis

Holotype, male, 17.0 mm: Eye rounded; head lobe shallow and not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxa 1 anteriorly produced, not shallower than coxa 2; coxae 1–5 shallower than the body plates; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm broadly oblique. Gnathopod 2, segment 2 not setose, segment 5 much shorter than segment 6, posterior margin narrow and lobed; segment 6, palm bearing a square process and defined by a tooth; dactyl not extending beyond the hand. Peraeopods 3 and 4, segment 4 not overhanging and hardly longer than segment 5. Peraeopod 5, segment 2 not posterodistally

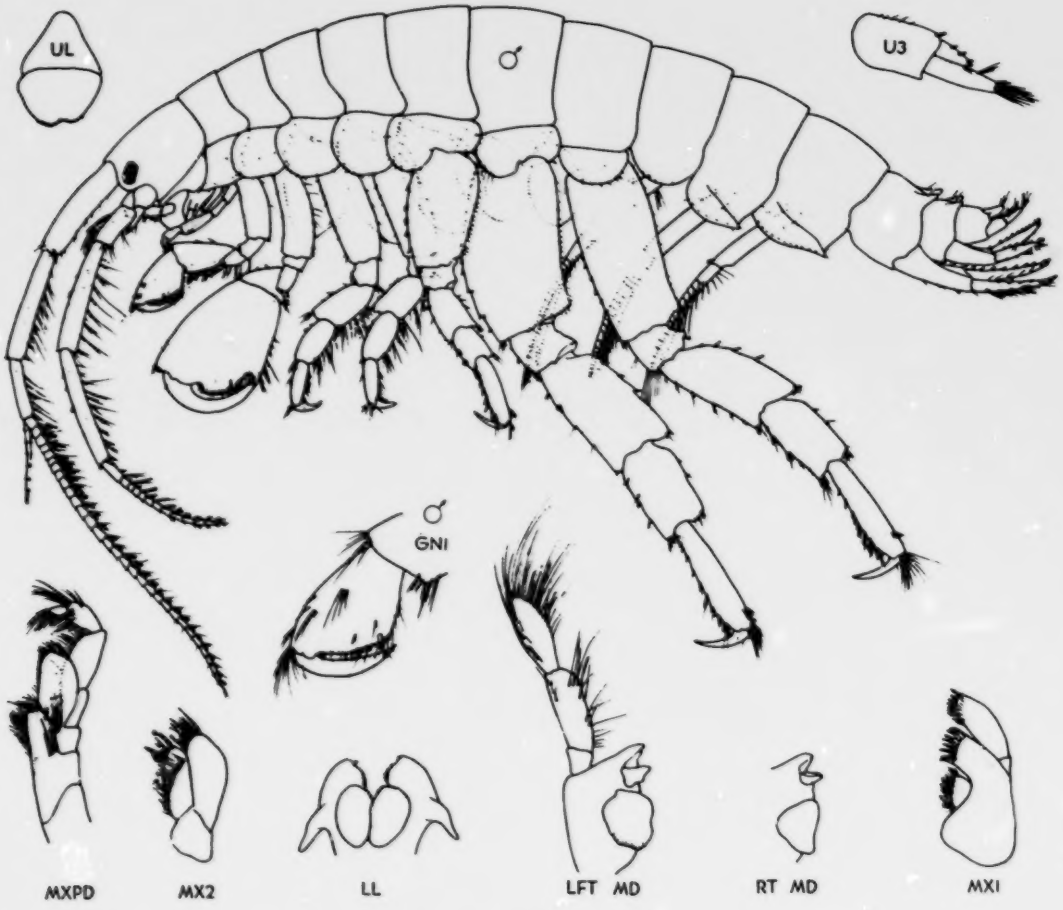


Figure 6. *Paroeurystheus tzvetkovae* n. sp. ♂ 17.0 mm, Constantine Harbour, Amchitka Is., Aleutian Is., Alaska.

notched and not greatly wider than segment 2 of peraeopods 6 and 7; segment 4 not expanded, hind margin not spinose. Peraeopod 6 enlarged, segment 2 anteriorly convex; segments 4 and 5 expanded. Peraeopod 7 enlarged, segment 2 narrow, margins parallel; segments 4 and 5 expanded. Urosome, segments 1 and 2 bearing dorsally a pair of setae and two strong cusps. Epimera 2 and 3 bearing a lateral ridge, posterodistal corner strongly notched. Uropod 1, peduncular spinous process about half the length of the longest ramus. Uropod 2, peduncular process present. Uropod 3, inner ramus half the length of the outer, terminally setose; outer ramus both medially and terminally setose. Telson terminating in two clusters of setae and a pair of small cusps.

Female: unknown.

Size: male 17.0 mm

Distribution

Known only for this locality.

Ecology

Data unavailable.

Remarks

The enlarged gnathopod 2 of the male, with shallow palmar protuberance and defining tooth, is a common feature of the genus, occurring also in *P. gurjanovae, P. anamae, P. latipes* and *P. sexdentatus*. All species show a tendency towards reduction of the third uropod inner ramus, to the greatest degree in *P. tzvetkovae* and *P. dentatus*. Enlargement and expansion of peraeopods 6 and 7 occurs in all species but *P. dentatus* and *P. gurjanovae*. This latter character is sexually related, developing only in subadult and mature males.

Etymology
Named in honour of N.L. Tzvetkova, the founder of the genus.

Genus *Podoceropsis* Boeck

Podoceropsis Boeck, 1861, p. 666; 1876, p. 583; Stebbing, 1888, p. 1108; Della Valle, 1893, p. 451 (part); Sars, 1894, p. 574, pl. 204; Stebbing, 1906, p. 618; J.L. Barnard, 1969a, p. 274; (subgenus) 1973, p. 18; Bousfield, 1973, p. 185.
Noenia Bate, 1862, p. 471.
Xenoclea Boeck, 1871, p. 243.

Type species:
Podoceropsis sophiae Boeck, 1861.

Additional species
Five species occur regionally: *P. amchitkensis* n. sp., *P. angustimana* n. sp., *P. barnardi* Kudryashov and Tzvetkova, *P. chionoecetophila*, n. sp., and *P. setosa* n. sp. The Atlantic *P. lindahlii*, once recorded in the Bering Sea (Shoemaker, 1955), is included for comparison.

Diagnosis
Body not dorsoventrally depressed. Head lobe acute, antennal sinus deep. Eye lenticular or oval. Antenna 1, peduncular segment 3 as long as segment 1, accessory flagellum microscopic; flagellum 1 subequal to flagellum 2. Upper lip, epistome produced. Mandibular palp quite broad, segment 3 clavate; molar with up to 8 raker spines. Maxilla 1 inner plate bearing a single terminal seta. Maxilla 2 bearing facial setae. Coxae short, lower margins not setose, not shallowing posteriorly. Coxa 1 not produced forward; coxae 1 and 2 (♂) hardly shallower than coxae 3–5, coxa 3 (♂) lacking stridulation ridges. Gnathopod 1, segment 5 not produced into a posterior lobe; segment 6 slender, palm transverse or indistinct, dactyl extending far beyond the palm. Gnathopod 2 (♂), segment 2 lacking stridulation ridges; segment 5 much shorter than segment 6 and narrowed posteriorly, although usually not into a lobe; palm not incised. Peraeopod 3, segment 4 twice as long or more than segment 5 and anterodistally produced. Peraeopod 5 (♂), segment 2 usually posterodistally notched; segment 4, hind margin concave; dactyl lacking an accessory tooth. Peraeopods 6 and 7 similar in form to but generally longer than peraeopod 5; segment 2, hind corner not setose; segment 5 bearing comb spines. Pleopods normal. Epimera not posterodistally notched and lacking a lateral ridge. Urosome dorsally bearing setae but not cusped. Uropod 1 bearing a peduncular spinous process; uropods 1 and 2 terminating in a group of spines. Uropod 3 ordinary, rami subequal, outer ramus terminating in setae, inner ramus terminating in a single spine. Telson bearing a pair of small apical cusps. Brood plates medium, oval or leaf-shaped; setae dense, hook-tipped.

Distribution
Broadly ranging in the north Atlantic and north Pacific.

Key to North Pacific Species of Podoceropsis

1. Head lobe strongly produced, rounded; eye reaching to edge of head lobe ..... *Podoceropsis lindahlii* Hansen, 1887
   Head lobe moderately to strongly produced, acute; eye not reaching to edge of head lobe 2
2. Gnathopod 2 (♂), dactyl not exceeding the hand; peraeopod 5 (♂), segment 2 posterodistally notched; gnathopod 2 (♀) similar in form to the ♂; palm with two teeth ..... *Podoceropsis chionoecetophila* n. sp. (page 22, fig. 10)
   Gnathopod 2 (♂), dactyl exceeding the palm; peraeopod 5 (♂), segment 2 not posterodistally notched; gnathopod 2 (♀) different in form to the ♂; palm with one or no teeth 3
3. Gnathopods 1 and 2, peraeopods 3 and 4 (♂), segment 2 setose; gnathopod 2 (♀), palm weakly excavate ..... *Podoceropsis setosa* n. sp. (page 24, fig. 11)
   Gnathopods 1 and 2, peraeopods 3 and 4 (♂), segment 2 barely or not setose; gnathopod 2 (♀), palm strongly excavate 4
4. Uropod 1, peduncular spinous process half the length of the longest ramus ..... *Podoceropsis amchitkensis* n. sp. (page 18, fig. 7)
   Uropod 1, peduncular spinous process one quarter the length of the longest ramus 5

5. Antenna 1 shorter than antenna 2; gnathopod 2 (♂), segment 6 rectangular, dactyl reaching, in oldest specimens, the full length of segment 6 .... *Podoceropsis angustimana* n. sp. (page 19, fig. 8)
Antennae 1 and 2 subequal; gnathopod 2 (♂), segment 6 oval, dactyl not more than half the length of segment 6 .... *Podoceropsis barnardi* (Kudryashov and Tzvetkova, 1975) (page 21, fig. 9)

Podoceropsis amchitkensis n. sp.
Figure 7

Material examined
St. Makarius Bay, Amchitka Island, Aleutian Islands, Alaska (51°22.8′N, 179°13.5′W) 1 ♂, 1 ♀. P.A. Lebednik Collection. Holotype, ♂, NMC-C-1981-912; allotype, ♀, NMC-C-1981-913; paratype, 1 ♀, NMC-C-1981-914.

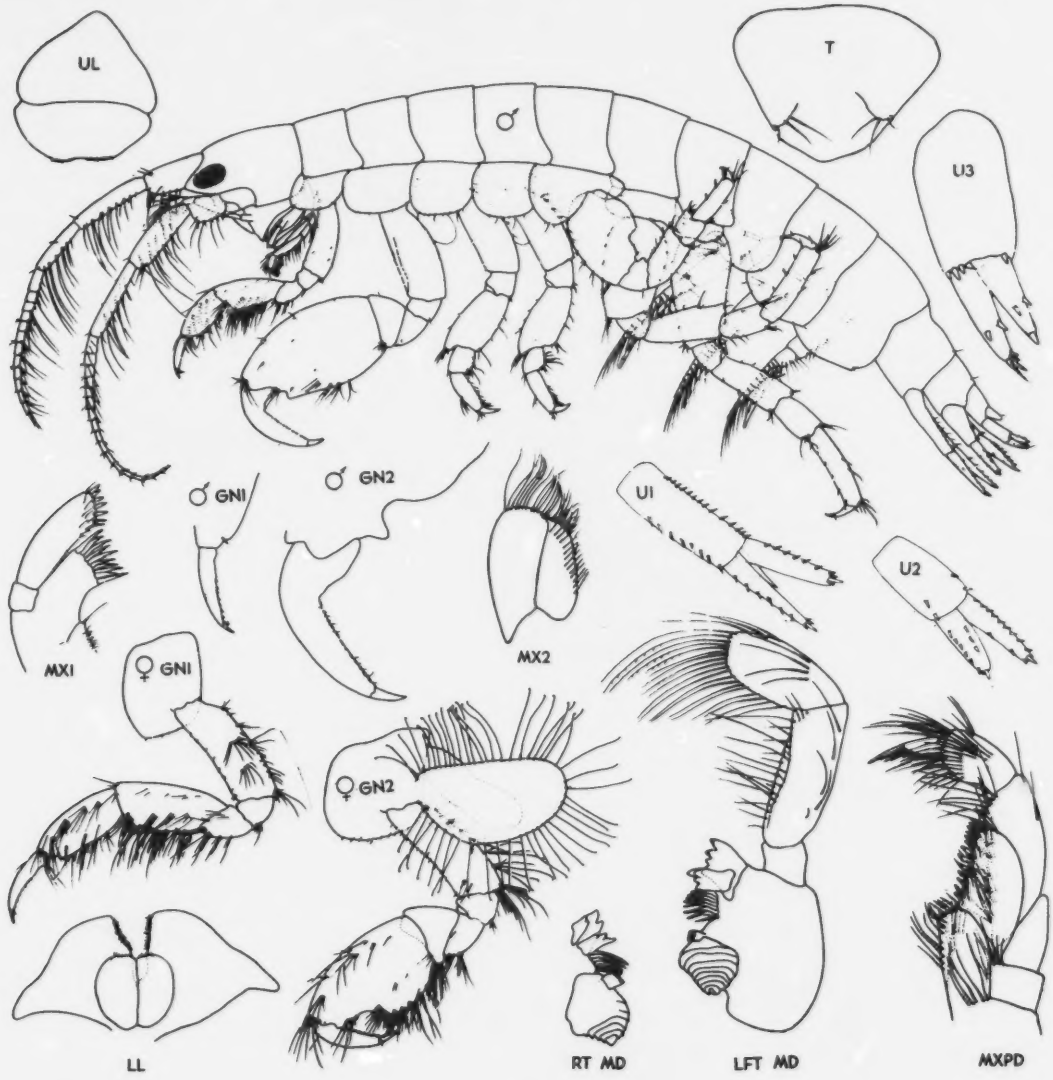


Figure 7. *Podoceropsis amchitkensis* n. sp. ♂ 6.0 mm, ♀ 6.0 mm, St. Makarius Bay, Amchitka Is., Alaska.

Diagnosis

Holotype, male, 7.0 mm: Eye oval; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxa 1 not markedly shallower than coxa 2; coxae 1–5 shallower than the body plates and increasing in depth posteriorly; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm indistinct. Gnathopod 2, segment 2 not setose; segment 5, posterior margin not produced into a lobe; segment 6, palm bearing a small medial process and defined by a tooth; dactyl not more than half the length of the palm. Peraeopods 3 and 4, segment 4 overhanging and more than twice the length of segment 5. Peraeopod 5, segment 2 posterodistally notched but hardly wider than segment 2 of peraeopods 6 and 7; segment 4 not expanded, hind margin not spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin not spinose. Urosome, segments 1 and 2 bearing a pair of setae but not dorsally notched. Epimera lacking a lateral ridge, posterodistal corner barely notched. Uropod 1, peduncular spinous process half the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal. Outer ramus only terminally setose. Telson terminating in a few setae and a cusp at each distal corner.

Allotype, female, 7.0 mm: Gnathopod 2, segment 6, palm excavate, defined by a spine. Peraeopod 5, segment 2 not notched.

Size range: male to 7.0 mm, female to 7.0 mm.

Distribution

Known only for this locality.

Ecology

Found in the littoral zone of a high salinity, protected outer coast beach, amongst rocks, boulders and kelp.

Remarks

This species differs from *P. angustimana* in the second gnathopod of the male by the shorter dactyl and broader, shorter segment 6; and longer spinous peduncular process of uropod 1 (in both sexes).

Etymology

In reference to the only known locality, Amchitka Island, Alaska.

Podoceropsis angustimana n. sp.

Figure 8

Material examined

Dodger Channel, southwest end of Diana Island. Barkley Sound, Vancouver Island, B.C. (48°50.4′N, 125°12.1′W) Bousfield 1976 stn. B27, 8 July 1976. 7.2–9.0 m dredge on sand, 12°C, 32+ ‰ .

Holotype, ♂, NMC-C-1981-909; allotype, ♀, NMC-C-1981-910; paratypes, 2♂♂, 3 ♀ ♀, 1 immature, NMC-C-1981-911.

Additional material

British Columbia — central mainland: 1 ♀ from Bousfield 1964 stn. H52; 4♂♂, 2 ♀ ♀ from Bousfield 1959 stn. V3, NMC cat.3042 (deposited in the Smithsonian Institution (USNM)); 8 ♂♂, 3 ♀ ♀, 2 immatures from Bousfield 1959 stn. V3, NMC Cat. 3043 (deposited in the Zoological Institute, Leningrad).

Diagnosis

Holotype, male, 4.8 mm: Eye lenticular; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 lacking a posterodistal spine. Upper lip, epistome produced. Coxa 1 not markedly shallower than coxa 2; coxae 1–5 shallower than the body plates and increasing in depth posteriorly; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm indistinct. Gnathopod 2, segment 2 not setose; segment 5, posterior margin not produced into a lobe; segment 6, palm bearing a process and defined by a tooth; dactyl increasing with age to the full length of the palm. Peraeopods 3 and 4, segment 4 overhanging and more than twice the length of segment 5. Peraeopod 5, segment 2 posterodistally notched but hardly wider than segment 2 of peraeopods 6 and 7; segment 4 distally expanded but hind margin not spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin not spinose. Urosome, segments 1 and 2 dorsally bearing a pair of setae but not notched. Epimera lacking a lateral ridge, posterodistal corner not notched. Uropod 1, peduncular spinous process a quarter the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal. Outer ramus only terminally setose. Telson terminating in a few setae and a cusp at each distal corner.

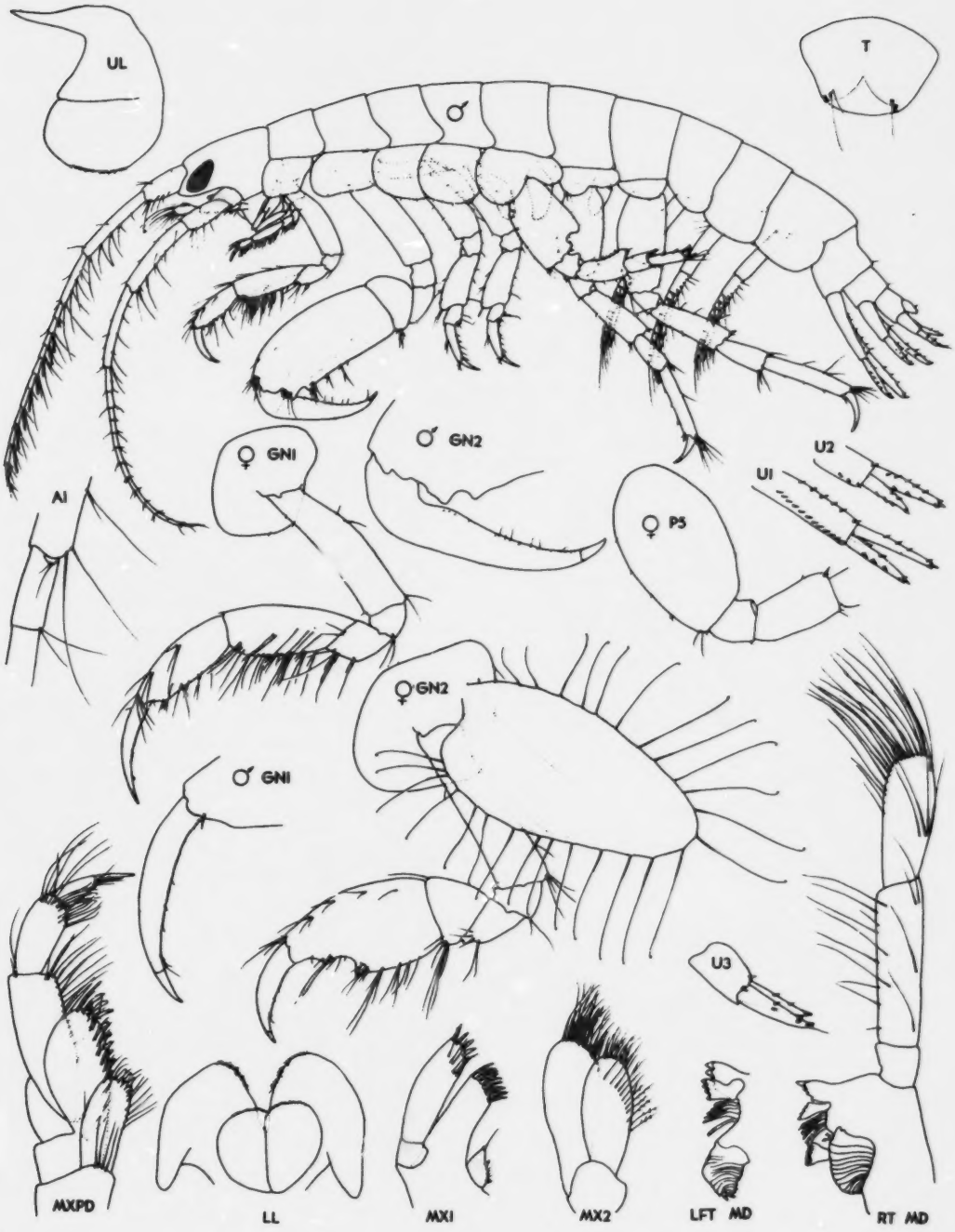


Figure 8. *Podoceropsis angustimana* n. sp. ♂ 4.8 mm, ♀ 4.5 mm, Dodger Channel, Barkley Sound, Vancouver Is., B.C.

Allotype, female, 4.5 mm: Gnathopod 2, segment 6, palm excavate, bearing a medial tooth and a defining spine. Peraeopod 5, segment 2 not notched, segment 4 normal.
Size range: male to 5.5 mm, female 4.5 to 6.5 mm.

Distribution:
Known only from central and southern B.C. (51°56′N, 128°29′W to 48°50.4′N, 125°12.1′W).

Ecology
Occurs on exposed and semi-exposed coasts in high salinity water subtidally from 11 to 72 m depth on sand bottoms.

Life history
Females ovigerous in August.

Remarks
This species closely resembles the more northerly *P. amchitkensis*, differing in the longer dactyl of the gnathopod 2 (mature male) and shorter peduncular process of uropod 1 (both sexes).

Etymology
L.: *angusti* = narrow; *mana* = hand, referring to the distinctive second gnathopod of the male.

Podoceropsis barnardi (Kudryashov and Tzvetkova)
Figure 9

Gammaropsis (Podoceropsis) barnardi Kudryashov and Tzvetkova, 1975, pp. 1306–9, fig. 1.

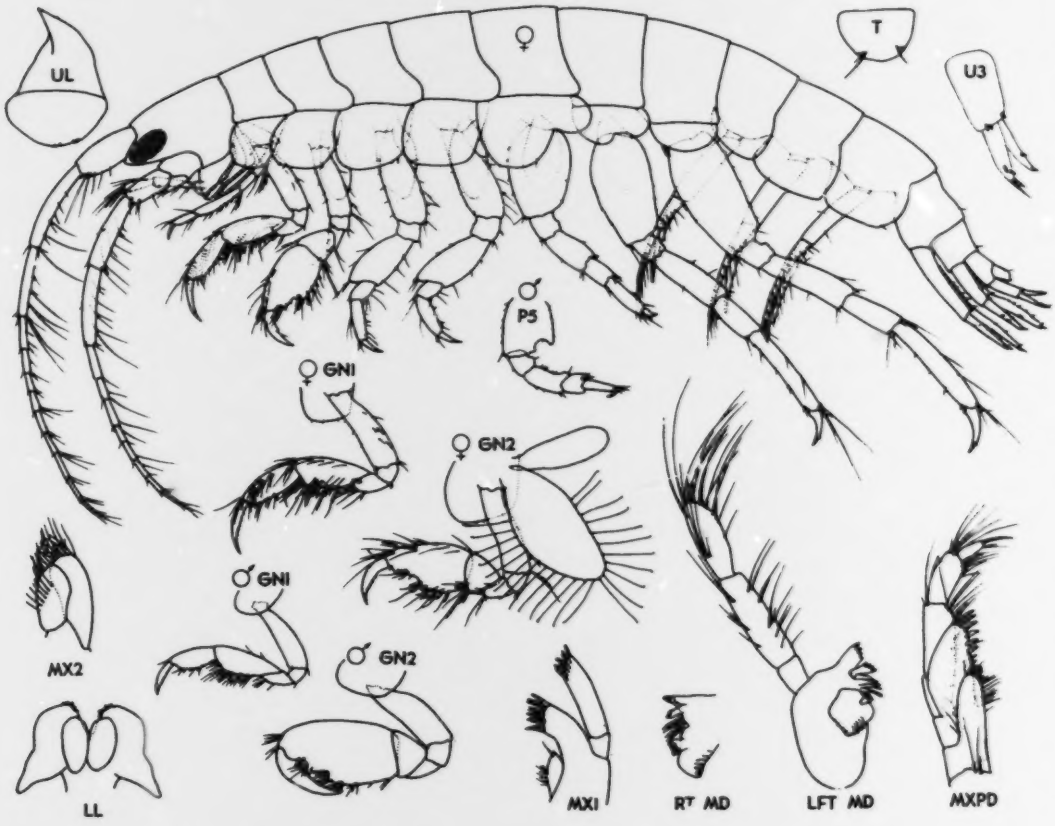


Figure 9. *Podoceropsis barnardi* Kudryashov and Tzvetkova ♂ 5.0 mm, ♀ 4.0 mm, jv ♀ antenna 2 - 3.5 mm, Trevor Channel, Barkley Sound, Vancouver Is., B.C.

Material examined

British Columbia — Vancouver Island: 3 ♀♀ from Bousfield 1975 stn. P22, Trevor Channel, 100 m off Cape Beale, Barkley Sound, Vancouver Is., B.C.; 17 m dredge over sand, shell and stones, 10°C, 33+ ‰. 9 August 1975.

Diagnosis:

Male: eye oval; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 bearing a small posterodistal spine. Upper lip, epistome produced. Coxa 1 not markedly shallower than coxa 2; coxae 1-5 shallower than the body plates and increasing in depth posteriorly; coxa 7 not expanded. Gnathopod 1, segment 2 barely setose and not produced into a posterodistal lobe; segment 6, palm indistinct. Gnathopod 2, segment 2 barely setose; segment 5, posterior margin not produced into a lobe; segment 6, palm bearing a process and a notch and defined by a sharp change of angle; dactyl longer than the palm. Peraeopods 3 and 4, segment 4 overhanging and more than twice the length of segment 5. Peraeopod 5, segment 2 strongly posterodistally notched but not wider than segment 2 of peraeopods 6 and 7; segment 4, hind margin concave. Paraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin not spinose. Urosome, segments 1 and 2 dorsally bearing a pair of setae. Epimera lacking a lateral ridge, posterodistal corner slightly notched. Uropod 1, peduncular spinous process only a quarter the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal; outer ramus terminally setose. Telson terminating in a few setae and a small cusp at each apex.

Female: coxa 1 not markedly shallower than coxa 2. Gnathopod 2, segment 6, palm excavate and defined by a spine. Peraeopod 5, segment 2 not notched, segment 4 normal. Other features as in the male.

Size range: male to 5.0 mm, female 4.0 to 5.5 mm.

Distribution

The species was first described from the southern and western Sakhalin, eastern U.S.S.R. (50°N, 145°E). The specimens collected at Cape Beale, Vancouver Is., B.C. (48°48′N, 125°12.5′W) are the first recorded for North America.

Ecology

Occurs in exposed and semi-protected coasts on sandy substrates at low water to 17 m depth.

Remarks

This species differs from the other British Columbia species of this group, *P. angustimana*, by the subequal antennae (both sexes), and by the broader second gnathopod with shorter dactyl (male).

Podoceropsis chionoecetophila n. sp.
Figure 10

Material examined

Coos Bay, Oregon, 600 m depth. Amongst eggs of the tanner crab *Chionoecetes tanneri*. Station #OBT 504 #43, 4 April 1973. P. Tester, coll. Holotype, ♂, NMC-C-1981-915; allotype, ♀, NMC-C-1981-916; paratypes, 10 ♂♂, 6 ♀♀, 37 immatures, NMC-C-1981-917.

Additional material

Alaska — Bering Sea near Amchitka Island (51°30′N, 179°16′E): 2 immatures from the collection of C.E. O'Clair, stn. 69 RD5; southeastern tip: 4♂♂, 9♀♀, 15 immature specimens from Bousfield and McAllister 1961 stns. A40, A92, A145 (60°13′N, 147°17′W).

Oregon — Coos Bay (43°25′N, 124°20′W) at 600 m depth — 13 ♂♂, 21 ♀♀, 52 immature specimens from the collection of P. Tester, at stns. OBT 504 #13 and #43; OBT 511 #22, 26, 28 (3 ♂♂, 3 ♀♀, 1 immature deposited in the Smithsonian Institution (USNM)); OBT 518 #18; OBT 557 #8 (3♂♂, 3 ♀♀, 7 immatures deposited in the Zoological Institute, Leningrad).

Diagnosis

Holotype, male, 6.5 mm: Eye oval; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxae 1 and 2 markedly shallower than coxae 3-5; coxae 1-5 slightly deeper than the body plates and increasing in depth posteriorly; coxa 7 not expanded. Gnathopod 1, segment 2 not setose and not produced into a posterodistal lobe; segment 6, palm transverse. Gnathopod 2, segment 2 weakly setose; segment 5, posterior margin produced into a lobe; segment 6, palm bearing a process and a small excavation and defined by a tooth; dactyl longer than the palm; subsequently a sharp change of angle on the hind margin of segment 6. Peraeopods 3 and 4, segment 4 overhanging and nearly twice the length of segment 5. Peraeopod

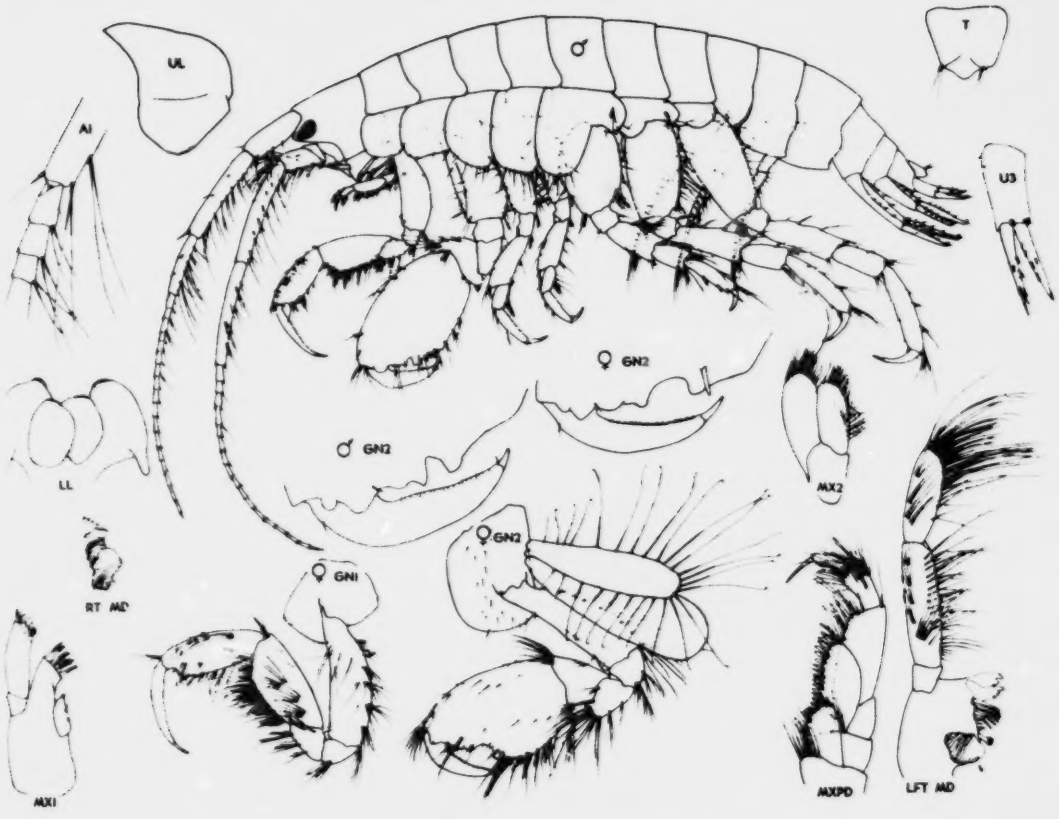


Figure 10. *Podoceropsis chionoecetophila* n. sp. ♂ 6.5 mm, ♀ 8.0 mm, Coos Bay, Oregon.

5, segment 2 only slightly posterodistally notched and not wider than segment 2 of peraeopods 6 and 7; segment 4 not expanded, hind margin not spinose. Peraeopods 6 and 7, segments 2, 4, 5 not expanded; segment 6, posterior margin not spinose. Urosome, segments lacking dorsal setae or notches. Epimera lacking a lateral ridge, posterodistal corner slightly notched. Uropod 1, peduncular spinous process only a quarter the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal; outer ramus terminally setose. Telson teminating in a few setae and a small cusp at each apex.

Allotype, female, 8.0 mm: Coxa 1 shallower than coxa 2. Gnathopod 2, segment 6, palm bearing a small tooth and broader excavation and defined by a spine. Peraeopod 5, segment 2 not notched. Other features similar to the male.

Size range: male to 7.0 mm, female 5.5 to 8.0 mm.

Distribution

The species is known only from these Alaska and Oregon locations.

Ecology

Apparently a commensal on the eggs of the tanner crab *Chionoecetes tanneri*, although in the Alaska samples there is no mention of an associate. It is a deep dwelling, cold water species, occurring at 36–79 m in Alaska and at 600 m in Oregon.

Life history

Females ovigerous April to July.

Remarks

This species closely resembles the Atlantic *P. nitida* which also is a crustacean commensal. Specimens of *P. nitida* are presently unavailable

to the author. However, comparison with the description and illustration of Sars (1894, p. 576, pl. 205, as *P. excavata*) indicates differences in the form of the antennae, first gnathopod, coxa 2 and peraeopods 5–7. Specifically, in *P. chionoecetophila*, the antennae are longer and less setose, segment 6 of the male gnathopod 1 is slenderer, the palm transverse and the dactyl longer; coxa 2 is shallower than coxa 3 and the hind margins of segment 2 of peraeopods 5–7 are more setose. A record of *Podoceropsis nitida* in the North Pacific (Sea of Okhotsk and Bering Sea — Margulis, 1963) deserves further analysis.

Podoceropsis setosa n. sp.
Figure 11

Material examined

A single ♀ from the Bering Sea near Amchitka Island, Aleutian Islands, Alaska (51°30′N, 179°16′W). Collection of C.E. O'Clair, 9 October 1969. Holotype, ♀, NMC-C-1981-970.

Diagnosis

Holotype, female, 7.5 mm: Eye oval; head lobe acute but not distally toothed. Antenna 1, peduncular segment 1 bearing a posterodistal spine. Upper lip, epistome produced. Coxa 1 not markedly shallower than coxa 2; coxae 1–5 shallower than the body plates but not increasing in depth posteriorly; coxa 7 not expanded. Gnathopod 1, segment 2 setose but not produced into a

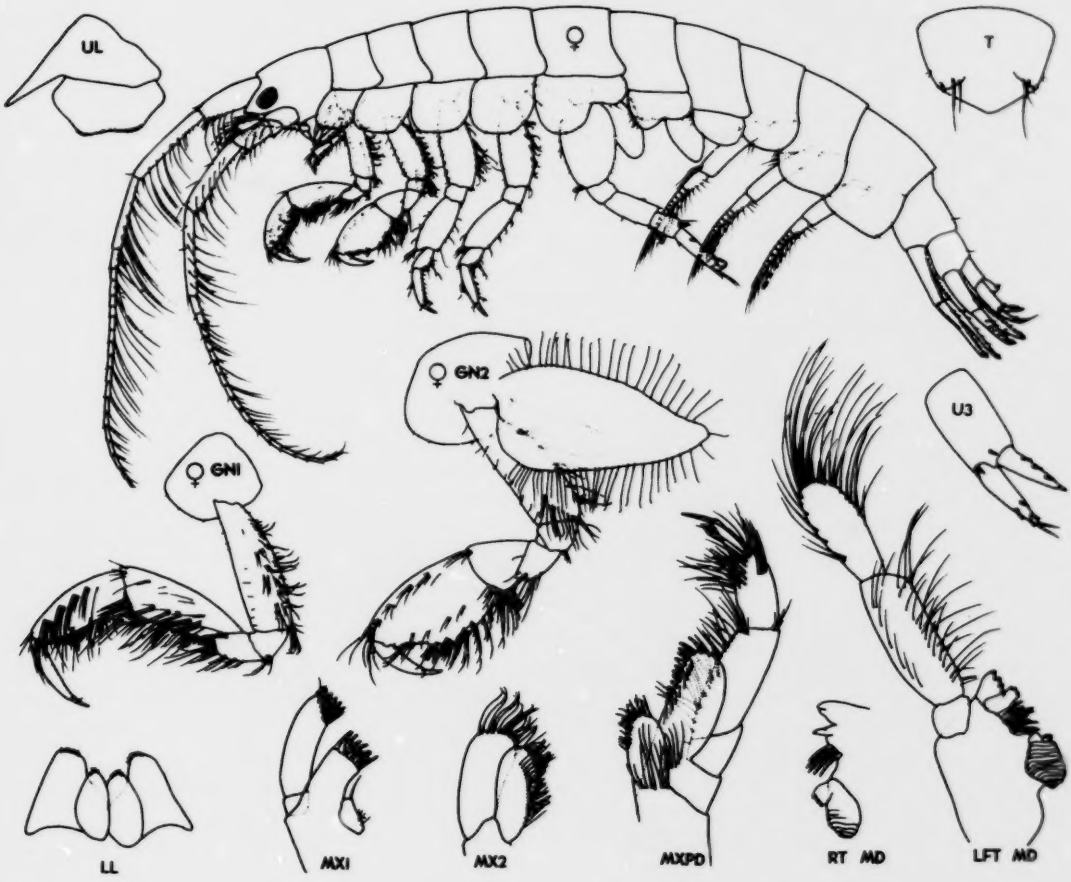


Figure 11. *Podoceropsis setosa* n. sp. ♀ 7.5 mm, Amchitka Is., Alaska.

posterodistal lobe; segment 6, palm indistinct. Gnathopod 2, segment 2 setose; segment 5, posterior margin not produced into a lobe; segment 6, palm slightly excavate and defined by a spine; dactyl hardly longer than the palm. Peraeopods 3 and 4, segment 4 overhanging and more than twice the length of segment 5. Peraeopod 5, segment 2 not posterodistally notched. Segment 4 not expanded, hind margin not spinose. Peraeopods 6 and 7 lost. Urosome, segments 1 and 2 bearing a pair of dorsal setae only. Epimera lacking a lateral ridge, posterodistal corner slightly notched. Uropod 1, peduncular spinous process half the length of the longest ramus. Uropod 2, peduncular process lacking. Uropod 3, rami subequal; outer ramus terminally setose. Telson terminating in a few setae and a cusp at each apex.
Male: unknown.

Distribution
Known only for this locality.

Ecology
Found in the littoral zone of a high salinity protected outer coast beach amongst rocks, boulders and kelp.

Remarks
Only one damaged specimen is known. The nearly unmodified second gnathopod may indicate that the specimen is not fully mature. By comparison with *P. amchitkensis*, the other known species of this group from Amchitka Island, *P. setosa* has much longer antennae.

Genus *Protomedeia* Krøyer

Protomedeia Krøyer, 1842, p. 154; Sars, 1894, p. 551; Stebbing, 1906, p. 623; J.L. Barnard, 1969a, p. 274; 1973, p. 22; Lincoln, 1979, p. 510.
Subgenus *Gammaropsis* (part) Liljeborg, 1855, p. 455.
Autonoe (part) Bruzelius, 1859, p. 23.

Type species
Protomedeia fasciata Krøyer, 1842.

Additional species
Approximately 17 species occur worldwide, of which five occur regionally: *P. articulata* J.L. Barnard, *P. fasciata* Krøyer, *P. grandimana* Brüggen, *P. prudens* J.L. Barnard, and *P. stephenseni* Shoemaker. The Californian *P. penates* J.L. Barnard may prove to be synonymous with *P. prudens*. In addition, five Russian species could ostensibly penetrate the northeastern Pacific community: *P. fascictoides* Bulytscheva, *P. popovi* Gurjanova, *P. coeca* Bulytscheva, *P. epimerata* Bulytscheva and *P. microdactyla* Bulytscheva. These are included in the keys for comparison.

Diagnosis
Body dorsoventrally depressed. Head lobe square, antenna 1 sinus shallow. Eye small to medium, round. Antenna 1, peduncular segment 3 shorter than segment 1; accessory flagellum multisegmented. Antenna 2 shorter than antenna 1, flagellum 1 shorter than flagellum 2. Upper lip, epistome moderately produced. Mandibular palp slender; molar with up to 2–3 raker spines. Maxilla 1, inner plate setose. Maxilla 2 lacking facial setae. Coxae shallow. Coxa 1 produced forward; coxae 1 and 2 (♂) not shallower than coxae 3–5; coxa 3 (♂) lacking stridulation ridges. Gnathopod 1, segment 5 not produced into a posterior lobe; palm distinct, dactyl much longer than the palm. Gnathopod 2 (♂), segment 2 lacking stridulation ridges; segment 5 subequal to or longer than segment 6 and not produced into a narrow posterior lobe; palm not incised. Peraeopod 3 and less so in peraeopod 4, anterior margin of segment 4 strongly setose (10 or more groups of setae in peraeopod 3); segment 4 not anterodistally overhanging segment 5, segment 5 half to two thirds the length of segment 4. Peraeopod 5 (♂), segment 2 not posterodistally notched; dactyl lacking an accessory tooth. Peraeopods 6 and 7 longer than peraeopod 5; segment 2, hind margin setose; segment 5 bearing comb spines. Pleopods, peduncles broad. Epimera not posterodistally notched, usually lacking a lateral ridge. Urosome dorsally smooth, bearing a pair of setae on segments 1 and 2. Uropod 1 bearing a peduncular spinous process; uropods 1 and 2 terminating in a group of spines; uropod 3, peduncle short; outer ramus a single segment, usually terminating in long spines; inner ramus usually two thirds to fully the length of the outer ramus. Telson bearing a pair of apical cusps or small spines. Brood plates narrow, elliptical; setae rather sparse, not hook-tipped. Medium size (regional species 4.5–14.0 mm).

Distribution
A large cold-water genus found in the North Atlantic, North Pacific and Arctic Oceans (Lincoln, 1979).

Key to Species of Protomedeia of the North Pacific (Males)

1. Uropod 3, inner ramus two thirds or less than the outer ramus 2
   Uropod 3, rami subequal 3
2. Gnathopod 1, segment 2 posterodistally produced into a lobe; gnathopod 2, segment 2 anteriorly flanged; coxa 5 not deeper than coxa 4; uropod spines short and stout ..... *Protomedeia fasciata* Krøyer, 1842 (page 28, fig. 13)
   Gnathopod 1, segment 2 not posterodistally produced into a lobe; gnathopod 2, segment 2 not anteriorly flanged; coxa 5 a third deeper than coxa 4; uropod spines long and slender ..... *Protomedeia articulata* J.L. Barnard, 1962 (page 27, fig. 12)
3. Gnathopod 1, palm transverse 4
   Gnathopod 1, palm oblique 9
4. Gnathopod 2, palm bearing a tooth 5
   Gnathopod 2, palm lacking a tooth 7
5. Gnathopods 1 and 2, hind margins not cusped; gnathopod 2, segment 5 not longer than segment 6, dactyl evenly curved, not overlapping the palm ..... *Protomedeia fasciatoides* Bulytscheva, 1952
   Gnathopods 1 and 2, hind margins cusped; gnathopod 2, segment 5 longer than segment 6, dactyl straight and slightly sinuous, greatly overlapping the palm 6
6. Gnathopod 2 bearing a coxal tooth at the junction of segment 2; peraeopods 3 and 4 slender; epimeron 2, hind corner squared ..... *Protomedeia prudens* J.L. Barnard, 1966[4] (page 31, figs. 15, 16)
   Gnathopod 2 lacking a coxal tooth at the junction of segment 2; peraeopods 3 and 4 thickened; epimeron 2, hind corner rounded ..... *Protomedeia penates* J.L. Barnard, 1966[4]
7. Gnathopod 2, palm oblique and defined by a large fixed tooth ..... *Protomedeia popovi* Gurjanova, 1951
   Gnathopod 2, palm transverse and defined only by a small spine or simply by a change of angle 8
8. Gnathopod 2, dactyl overlapping the palm by nearly half its full length; uropod 3, outer ramus bearing 3 short medial spines and a tuft of terminal setae ..... *Protomedeia coeca* Bulytscheva, 1952
   Gnathopod 2, dactyl not overlapping the palm by more than the unguis; uropod 3, outer ramus bearing up to 10 long medial spines which merge into long terminal setae ..... *Protomedeia stephenseni* Shoemaker, 1955 (page 33, fig. 17)
9. Gnathopod 2, palm bearing a large notched process, dactyl overlapping the palm by up to 30% of the full length; coxae 1–5, margins barely setose ..... *Protomedeia grandimana* Brüggen, 1905 (page 29, fig. 14)
   Gnathopod 2, palm bearing a shallow process or lacking one; dactyl not overlapping the palm; coxae 1–5, margins strongly setose 10
10. Gnathopod 2, segment 5 longer and broader than segment 6 ..... *Protomedeia epimerata* Bulytscheva, 1952
    Gnathopod 2, segment 5 not larger than segment 6 ..... *Protomedeia microdactyla* Bulytscheva, 1952

Key to the Northeastern Pacific Species of Protomedeia (both sexes) (Alaska to California)

1. Uropod 3, inner ramus two thirds or less the length of the outer ramus 2
   Uropod 3, inner ramus nearly as long as the other ramus 3

[4] *Protomedeia prudens* and *P. penates* may prove to be different growth stages of the same species.

2. Uropods 1–3, spines short and stout; gnathopod 1 (♂), segment 2 posterodistally produced into a lobe; gnathopod 2 (♂), segment 2 anteriorly flanged; coxa 5 (♂) not deeper than coxa 4; gnathopod 2 (♂), palm transverse .... *Protomedeia fasciata* Krøyer, 1842 (page 28, fig. 13)
Uropods 1–3, spines long and slender; gnathopod 1 (♂), segment 2 not posterodistally produced into a lobe; gnathopod 2 (♂), segment 2 not anteriorly flanged; coxa 5 (♂) a third deeper than coxa 4; gnathopod 2 (♀), palm oblique .... *Protomedeia articulata* J.L. Barnard, 1962 (page 27, fig. 12)
3. Antenna 1 hardly longer than antenna 2; gnathopods 1 and 2 (♂), segment 6 distally tapered, hind margin cusped; gnathopod 2 (♂), dactyl straight and slightly sinuous; coxa 5 (♂) a third deeper than coxa 4; gnathopod 2 (♀), palm oblique .... *Protomedeia prudens* J.L. Barnard, 1966 (page 31, figs. 15, 16)
Antenna 1 a third longer than antenna 2; gnathopods 1 and 2 (♂), segment 6 not distally tapered, hind margin not cusped; gnathopod 2 (♂), dactyl evenly curved; coxa 5 (♂) not deeper than coxa 4; gnathopod 2 (♀), palm transverse 4
4. Maxilla 1 palp lacking a setal group on segment 1; coxae 1–5, lower margin barely setose; gnathopod 1, palm oblique; gnathopod 2 (♂) enlarged, palm oblique and bearing a broad protuberance .... *Protomedeia grandimana* Brüggen, 1905 (page 29, fig. 14)
Maxilla 1 palp bearing a setal group on segment 1; Coxae 1–5, lower margin densely setose; gnathopod 1, palm transverse; gnathopod 2 (♂) hardly enlarged, palm transverse and lacking a protuberance .... *Protomedeia stephenseni* Shoemaker, 1955 (page 33, fig. 17)

Protomedeia articulata J.L. Barnard
Figure 12

Protomedeia articulata J.L. Barnard, 1962, pp. 48–50, fig. 21.

Material examined
Oregon: 2 ♂♂, 2 ♀ ♀, 3 immatures from the collections of Oregon State University, stn. MCR 958 and LBXC 006 (2–3) (46°13′N, 124°90′W and 44°26.4′N, 124°14.6′W respectively); 1♂ and 1 subadult ♀ from the collection of J. Trautman stns. LBXC 197 and 214 (same locality).

Diagnosis
Male: antenna 1 longer than antenna 2; peduncular segment 3 more than half the length of segment 1; antenna 2 weakly setose. Maxilla 1 bearing a setal group at the base of the palp. Margins of coxae 1–5 barely setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 longer than segment 6; segment 6, hind margin not cusped, palm rounded transverse. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxa; segment 5 longer and wider than segment 6; segment 6 distally tapered, hind margin not cusped, palm transverse, bearing a medial tooth and an articulating defining spine; dactyl evenly curved and overlapping the palm by a third of its full length. Peraeopods 3 and 4, anterior margin of segment 4 densely setose, segment 4 not anterodistally produced over segment 5; dactyl shorter than segment 6. Peraeopod 5, coxa deeper than coxae 1–4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus two thirds the length of the outer, spines long and slender.
Female: gnathopod 2, segment 5 subequal to segment 6, palm oblique, dactyl not overlapping the palm. Other features similar to the male.
Size range: male to 8.0 mm; female 5.5 to 7.0 mm.

Remarks
This is the only regional species that lacks a group of setae on segment 1 of the maxilla 1 palp.

Distribution
Oregon (46°13′N, 124°90′W) to La Jolla, California (32°52′N, 117°16′W).

Ecology
Occurs subtidally from 9 to 906 m on the exposed coastal shelf and in submarine canyons.

Life history
Females ovigerous in June.

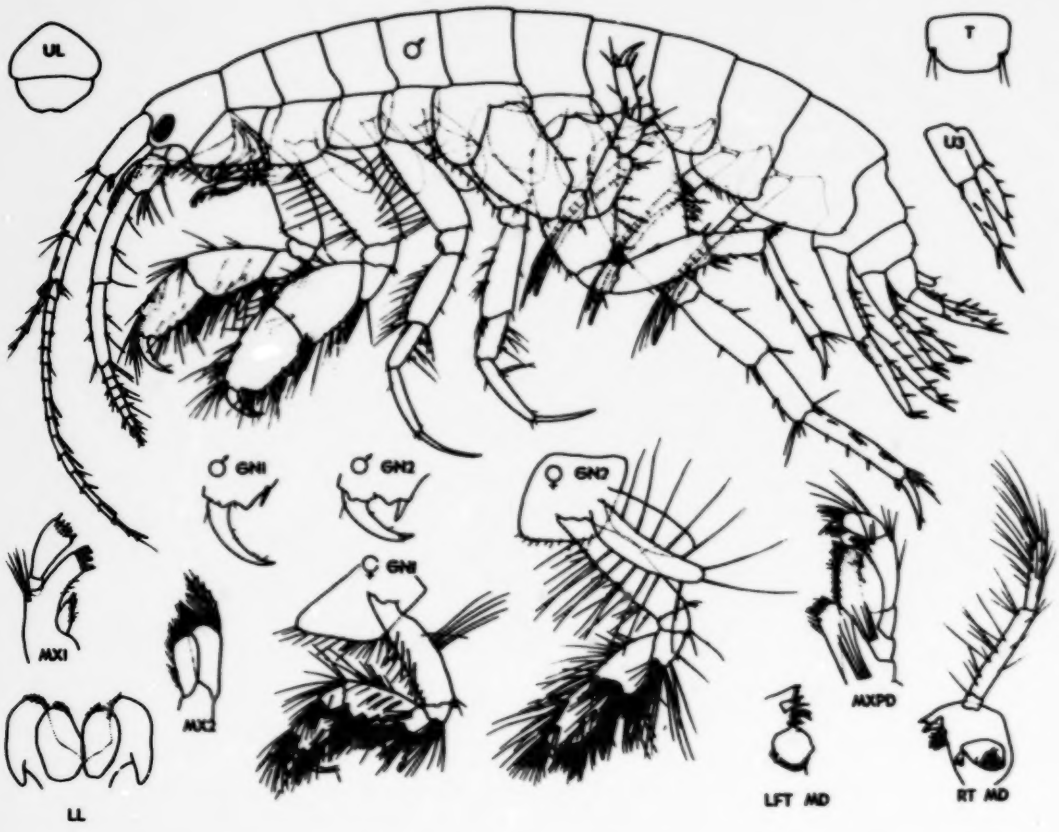


Figure 12. *Protomedeia articulata* Barnard ♂ 4.5 mm, (antenna 1 from a juvenile, 3.5 mm), ♀ 7.0 mm, Clatsop Co., Oregon.

Protomedeia fasciata Krøyer
Figure 13

> *Protomedeia fasciata* Krøyer, 1842, p. 154; Sars, 1894, p. 552, pl. 196; Stebbing, 1906, p. 623; Stephensen, 1942, p. 376; Schellenberg, 1942, p. 199; Gurjanova, 1951, pp. 859–862, figs. 603, 604; Shoemaker, 1955, pp. 58–60, fig. 17; Lincoln, 1979, pp. 510–511, fig. 245.

Material examined

Alaska — Bering Sea: northeast of St. Lawrence Island (64°N, 169°W) approximately 100 specimens from P. Slattery 1980 stn. 2, (2♂♂, 11 ♀♀, 5 immatures deposited in the Smithsonian Institution (USNM)), and from stn. 23 (1 ♂, 1 ♀ deposited in the Zoological Institute, Leningrad).

Diagnosis

Male: antenna 1 slightly longer than antenna 2; peduncular segment 3 less than half the length of segment 1; antennae 2 moderately setose. Maxilla 1 bearing a setal group at the base of the palp. Margins of coxae 1–5 weakly setose. Gnathopod 1, segment 2 posterodistally produced into a lobe; segment 5 as long as segment 6; segment 6, hind margin not cusped, palm transverse. Gnathopod 2, segment 2 anteriorly flanged, but lacking a posterior tooth at the junction of the coxa; segment 5 longer and wider than segment 6; segment 6 distally tapered, hind margin cusped, palm transverse, bearing a medial tooth and an articulating defining spine; dactyl evenly curved and overlapping the palm by little more than the unguis. Peraeopods 3 and 4, anterior margin of segment 4 densely setose, segment 4 not anterodistally produced over segment 5, dactyl shorter than segment 6. Peraeopod 5, coxa not deeper than coxae 1–4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus two thirds the length of the outer, spines short and stout.

Female: gnathopod 1, segment 2 not posterodistally lobed. Gnathopod 2, segment 2 not anteriorly

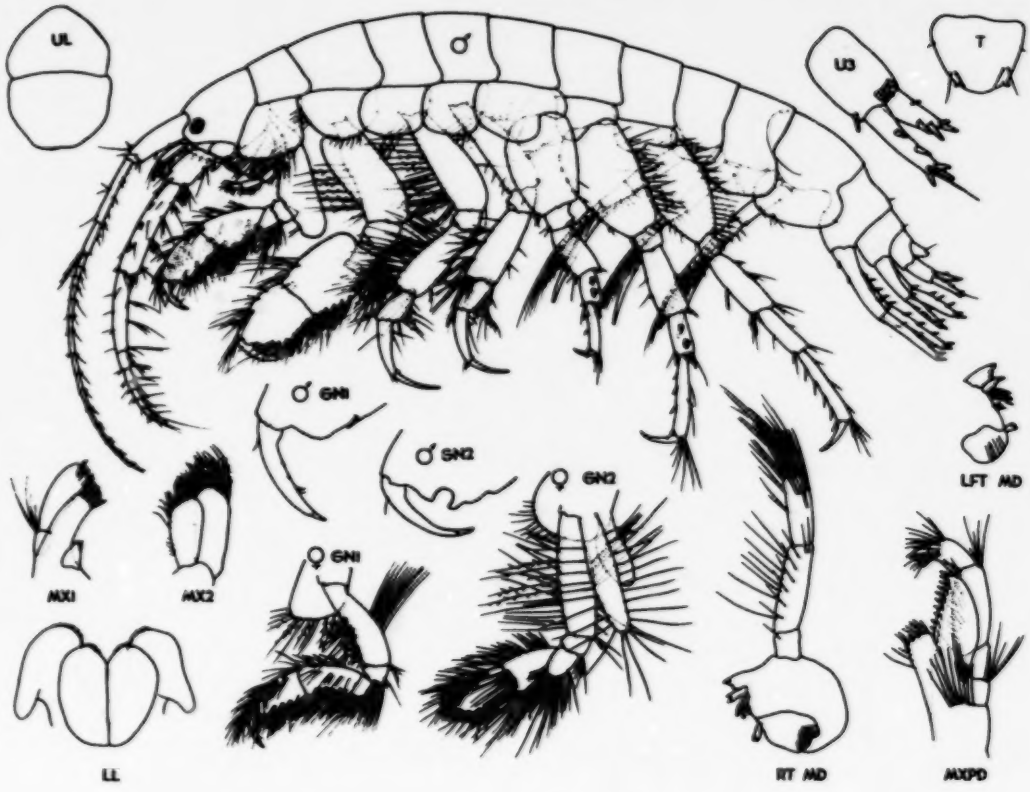


Figure 13. *Protomedeia fasciata* Kröyer ♂ 5.5 mm, ♀ 6.0 mm, St. Lawrence Is., Alaska.

flanged; segment 5 little wider than segment 6; segment 6 distally tapered; palm transverse, but lacking a medial tubercle; dactyl not overlapping the palm. Other features similar to the male.
Size range: male to 8.0 mm, female 5.5 to 8.0 mm.

Distribution
Bering Sea, Okhotsk Sea, U.S.S.R., Arctic Ocean, North Atlantic (American and European coasts), North Sea, British Isles.

Ecology
A cold water species recorded subtidally from 5 to 150 m.

Life history
Females ovigerous in July.

Protomedeia grandimana Brüggen
Figure 14

Protomedeia grandimana Brüggen, 1905, p. 223, fig. 5; 1907, p. 233, figs. 8, 9; Stebbing, 1906, p. 738; Stephensen, 1942, p. 379 (part), fig. 57; 1944, p. 122; Shoemaker, 1955, p. 59, fig. 17; Gurjanova, 1951, pp. 862–863, fig. 605.

Material examined
Alaska — Bering Sea: approximately 600 specimens from St. Lawrence Is., stns. 2, 5, 23, J. Emery, F.H. Fay and P. Slattery, collectors. Southeastern tip — approximately 100 specimens from Bousfield 1980 stn. S17F1; approximately 100 specimens from Bousfield and McAllister stns. A74, A83, A91, A153; 2 specimens from the collection of F.H. Fay, 1965.
British Columbia — Vancouver Island and southern mainland: 3 specimens from Bousfield 1978 stns. V5, V6; 1 specimen from Bousfield 1955 stn. EB5; 4 specimens from Bousfield stn. F9; ap-

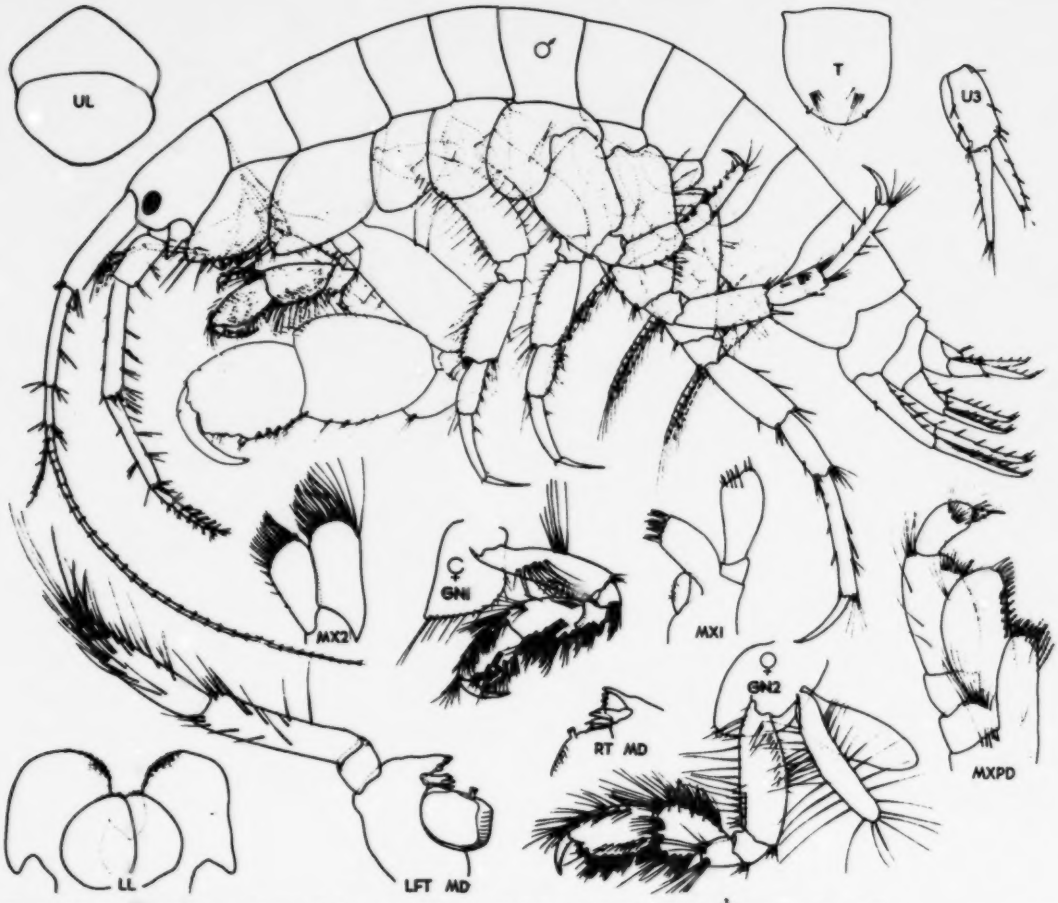


Figure 14. *Protomedeia grandimana* Brüggen ♂ 10.0 mm, ♀ 8.0 mm, Saanich Inlet, Vancouver Is., B.C.

proximately 200 specimens from the collections of K.E. Conlan, C.D. Levings and C. Low (1 ♂, 4 ♀♀, 4 immatures from NMC accession no. 1979–126, Saltspring Is., B.C., deposited in the Smithsonian Institution (USNM), and 1 ♂, 2 ♀♀, 5 immatures from the same collection deposited in the Zoological Institute, Leningrad)

Diagnosis

Male: antenna 1 nearly a third longer than antenna 2, peduncular segment 3 less than half the length of segment 1; antenna 2 weakly setose. Maxilla 1 lacking a setal group at the base of the palp. Margins of coxae 1–5 weakly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 subequal to segment 6; segment 6, hind margin not cusped, palm oblique. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxa; segment 5 longer and broader than segment 6; segment 6 not distally tapered, hind margin not cusped, palm oblique, bearing a wide medial protuberance and a small articulating defining spine; dactyl evenly curved and overlapping the palm by up to half its full length. In very old males the palmar defining spine is lost and the dactyl curves inwards along the medial surface of segment 6. Peraeopods 3 and 4, anterior margin of segment 4 densely setose, segment 4 not anterodistally produced over segment 5, dactyl shorter than segment 6. Peraeopod 5, coxa not deeper than coxae 1–4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus nearly as long as the outer, spines long and slender.

Female: gnathopod 2, segment 5 shorter and hardly wider than segment 6; segment 6 not distally tapered, palm oblique and lacking a medial protuberance; dactyl overlapping the palm by little more than the unguis. Other features similar to the male.

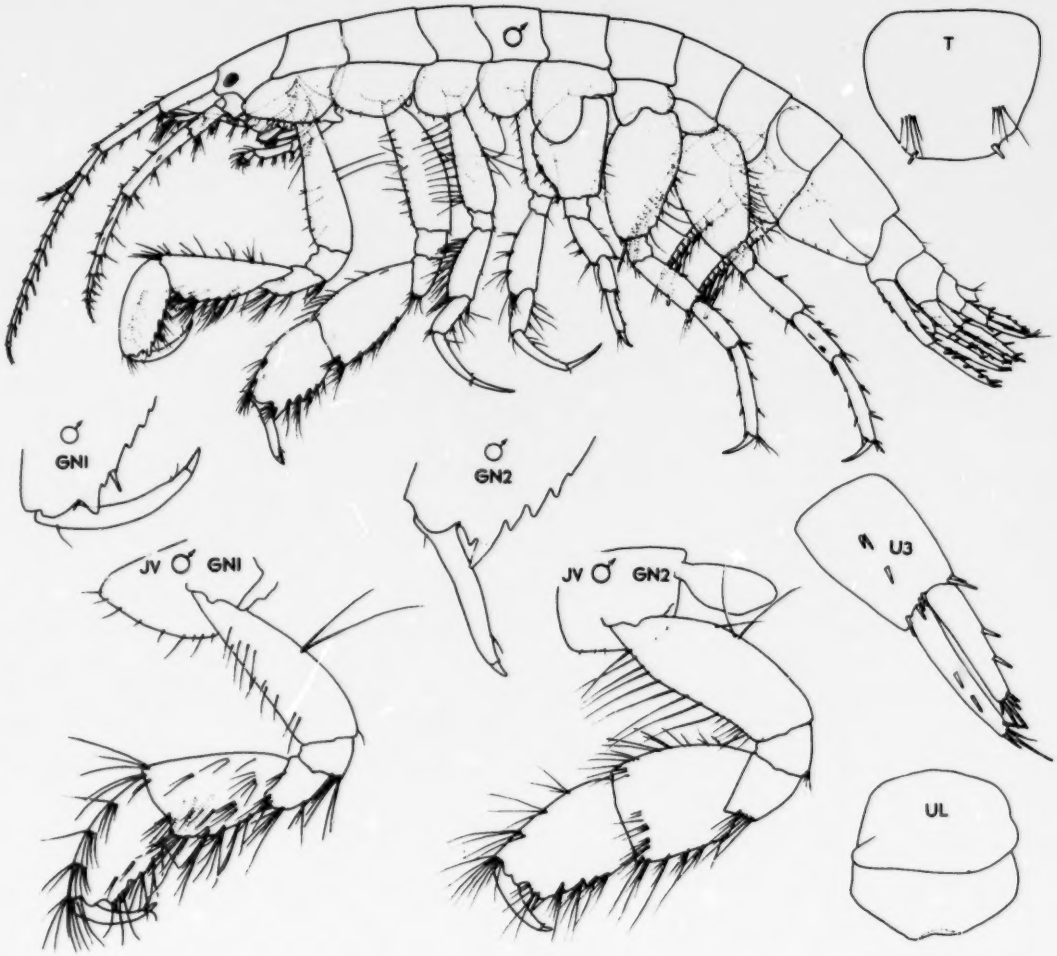


Figure 15. *Protomedeia prudens* Barnard ♂ 6.0 mm, jv ♂ 4.5 mm, Hope Is., Vancouver Is., B.C.

Size range: male to 10.5 mm, female 6.0 to 10.0 mm.

Distribution
St. Lawrence Island, Bering Sea (64°N, 169°W) to southern B.C. (48°50′N, 123°50′W); also recorded from the Sea of Okhotsk, U.S.S.R. and from the Murman Coast, Kara Sea, Spitzbergen. Shoemaker (1955) cautions that many of the localities assigned to this species by Stephensen (1942, pp. 384 and 385) likely apply only to *Protomedeia stephenseni.*

Ecology
A cold-water species occurring at low water to 200 m depth on semi-protected coasts. Summer temperatures recorded in the collections of Bousfield, 1961 to 1980, were 9.6 to 15.7°C, salinities 14.3 to 29.0 ‰. This species has also been found in the stomach of the gray whale *(Eschrichtius glaucus)* (F.H. Fay, collection data).

Life history
Female ovigerous in April to August.

Protomedeia prudens J.L. Barnard
Figure 15 and 16

Protomedeia prudens J.L. Barnard, 1966, p. 83, fig. 36; 1971, p. 15–17, figs. 11, 12.

Material examined
British Columbia — Queen Charlotte Islands and northern mainland: 3 specimens from Bousfield

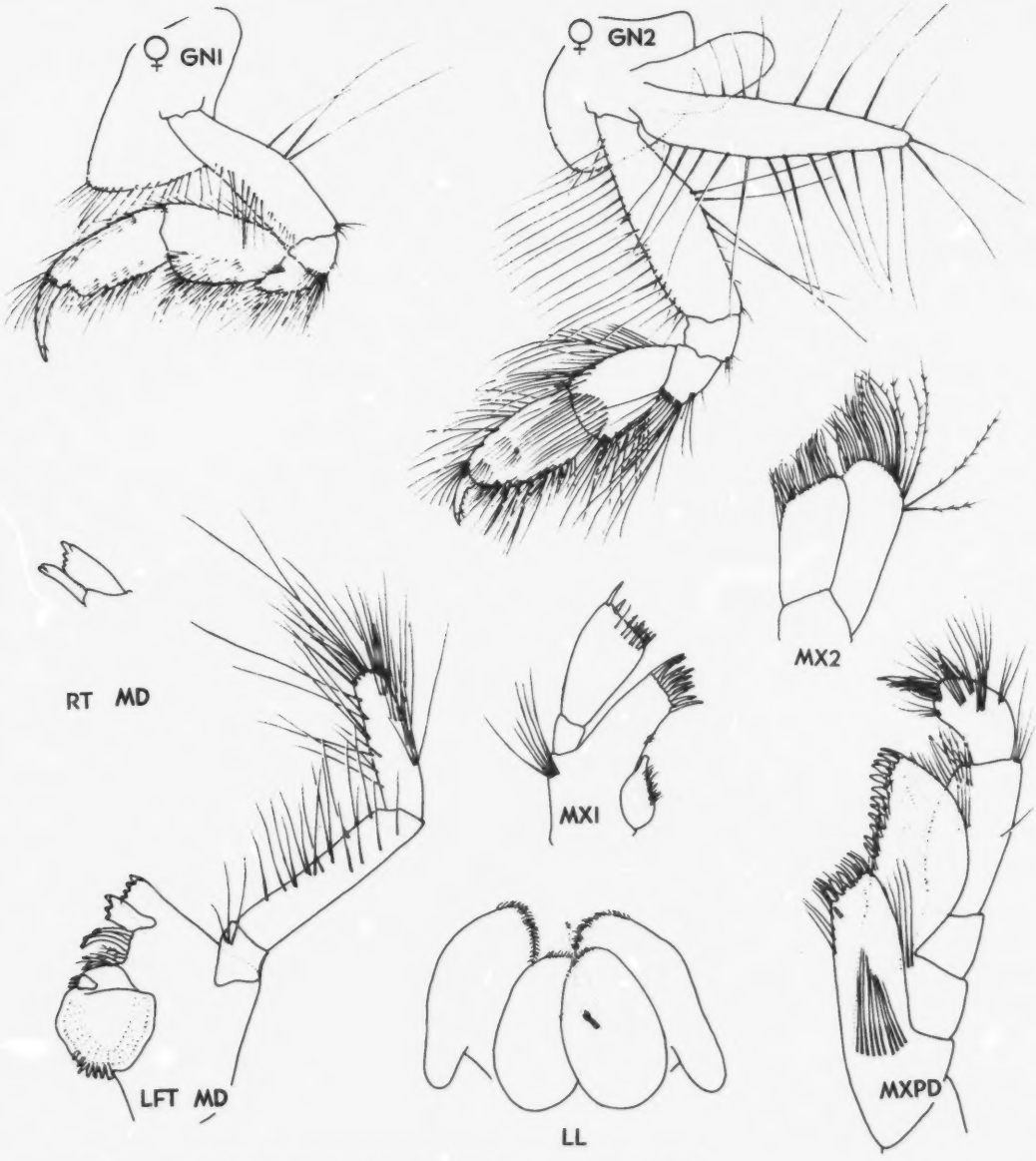


Figure 16. *Protomedeia prudens* Barnard ♀ 7.0 mm, Hope Is., Vancouver Is., B.C.

1964 stn. H40 and H49; 1 specimen from Bousfield 1957 stn. E14c. Vancouver Island and southern mainland: 13 specimens from Bousfield 1978 stns. B8, B9, V1, V2, V5, V6; 30 specimens from Bousfield 1977 stns. B1, B13, B14, E1, E3, E5, P2, P3, P8; 8 specimens from Bousfield 1976 stns. B8, B9e, B10c, B27, EB5, EB8; 63 specimens from Bousfield 1959 stns. N16, N22, O13, V3; 1 specimen from Bousfield 1955 stn. F6; 35 specimens from the collections of G.C. Carl, K.E. Conlan, D.V. Ellis, J.F.L. Hart, C.D. Levings and P. O'Rourke.

Washington — approximately 150 specimens from Bousfield 1966 stns. W13 (deposited in the Smithsonian Institution (USNM)), and W39 (deposited in the Zoological Institute, Leningrad).

Oregon — 6 specimens from Oregon State University Cruise C7506C.

Diagnosis

Male: antenna 1 slightly longer than antenna 2, peduncular segment 3 less than half the length of segment 1; antenna 2 weakly setose. Maxilla 1 bearing a setal group at the base of the palp. Margins of coxae 1–5 weakly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 longer than segment 6; segment 6, hind margin cusped, palm transverse. Gnathopod 2, segment 2 not anteriorly flanged but bearing a posterior tooth at the junction of the coxa; segment 5 longer and wider than segment 6; segment 6 distally tapered, hind margin cusped, palm transverse, bearing a medial tooth and an articulating defining spine; dactyl straight and slightly sinuous and overlapping the palm by more than half its full length. Peraeopods 3 and 4, anterior margin of segment 4 densely setose, segment 4 not anterodistally produced over segment 5, dactyl shorter than segment 6. Peraeopod 5, coxa deeper than coxae 1–4; segment 2 anteriorly bulged. Epimera bearing a lateral ridge. Uropod 3, inner ramus slightly shorter than the outer, spines slender.

Juvenile male: gnathopod 1, segment 5 broader and subequal to segment 6, hind margin of segment 6 not cusped, dactyl shorter than in the adult; gnathopod 2, coxal tooth lacking, segment 5 shorter and broader than in the adult, segment 6 not posteriorly cusped, dactyl shorter and evenly rounded.

Female: gnathopods 1 and 2, hind margin of segment 6 not cusped; gnathopod 2, segment 5 wider than segment 6; segment 6 distally tapered, palm oblique and lacking a medial tooth; dactyl not overlapping the palm. Other features similar to the male.

Size range: male to 6.0 mm, female 4.5 to 7.5 mm.

Remarks

On comparison of type specimens, this species was found to be exceedingly similar to *P. penates* J.L. Barnard, 1966. Differences cited by Barnard (1966) for differentiation of the latter species from *P. prudens* (e.g. thickened segment 4 of peraeopods 1 and 2, an obliquely rounded posteroventral corner of pleonal epimeron 2, larger coxae and stouter and shorter fifth segments of gnathopods 1 and 2 in *P. penates*) may prove to be the result of instar variation.

Distribution

Skidegate Inlet, Queen Charlotte Islands, B.C. (53°14′N, 131°54′W) to La Jolla Canyon (32°52′48″N, 117°16′32″W).

Ecology

A subtidal species, recorded to 400 m depth, but sometimes also found at low-water, generally on mud or sand of protected and semi-protected coasts. Summer temperatures recorded in the collections of Bousfield, 1957–1978, were 10.4 to 14°C, salinities 25.6–32.7 °/oo

Life history

Females ovigerous in April to August.

Protomedeia stephenseni Shoemaker
Figure 17

Protomedeia stephenseni Shoemaker, 1955 pp. 60–63, fig. 18.
Protomedeia grandimana: Stephensen, 1942, p. 379 (part), figs. 58, 59.

Material examined

Alaska – Bering Sea: northeast of St. Lawrence Island (64°N, 169°W) 2 juvenile ♂♂, 3 subadult ♀♀ from stn. 23, 3 subadult ♀♀ from stn. 2, P. Slattery Collection.

Diagnosis

Male: antenna 1 a third longer than antenna 2; peduncular segment 3 less than half the length of segment 1. Antenna 2 moderately setose. Maxilla 1 bearing a setal group at the base of the palp. Margins of coxae 1–5 strongly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 longer than segment 6; segment 6, hind margin not cusped, palm transverse. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxae; segment 5 subequal to and slightly wider than segment 6; segment 6 not distally tapered, hind margin not cusped, palm transverse, and lacking both a medial tooth and an articulating defining spine; dactyl evenly curved and not overlapping the palm. Peraeopods 3 and 4, anterior margin of segment 4 densely setose, segment 4 not anterodistally produced over segment 5, dactyl not longer than segment 6. Peraeopod 5, coxa somewhat deeper than coxae 3–4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus three-quarters the length of the outer, spines long and slender.

Female: gnathopod 2, segment 5 subequal to segment 6; segment 6 not distally tapered, palm transverse, dactyl not overlapping the palm. Other features similar to the male.

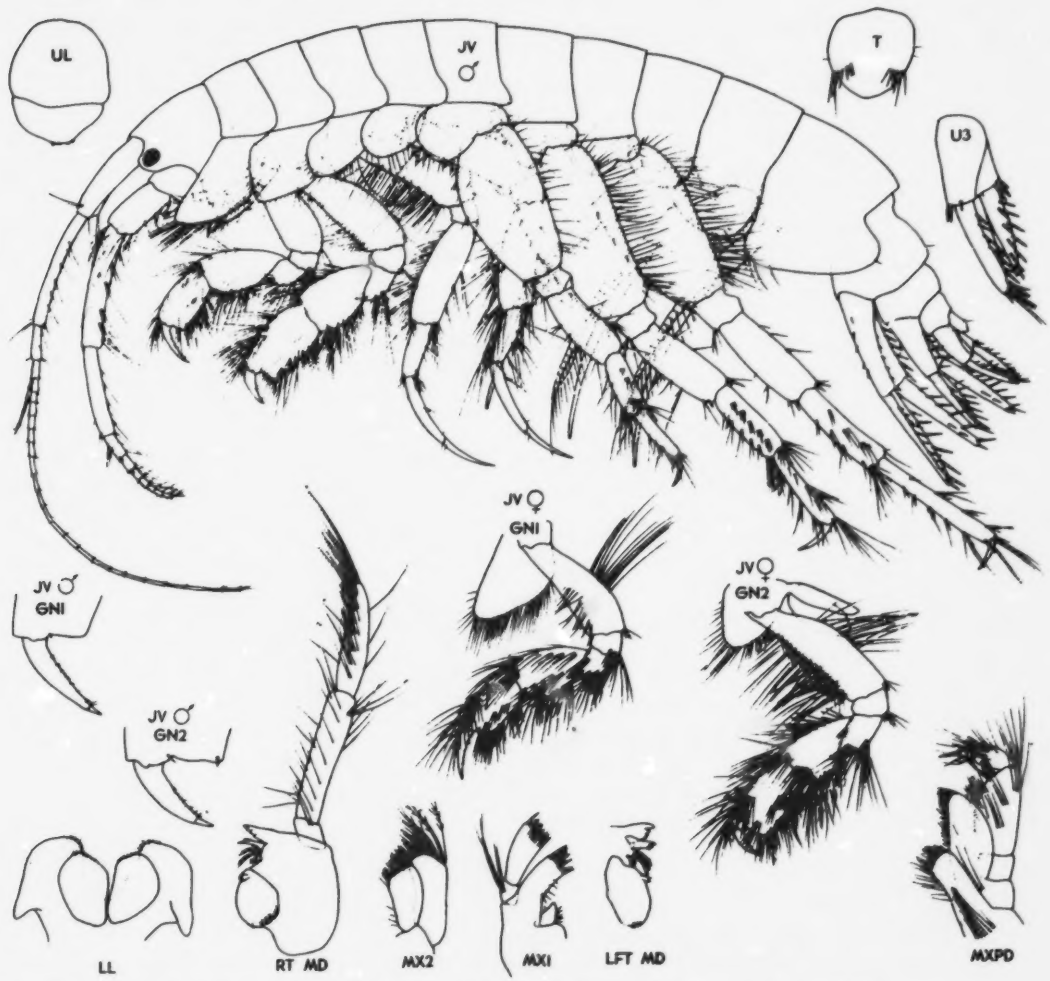


Figure 17. *Protomedeia stephenseni* Shoemaker jv. ♂ 10.5 mm, jv ♀ 12.5 mm, St. Lawrence Is., Alaska.

Size range: male, to 14.0 mm; female, 13.0 to 14.0 mm.

Distribution

Bering Sea, Pt. Barrow, Alaska, East Iceland, North Norway, Greenland. Shoemaker (1955) cautions that many of the localities given to this species by Stephensen (1942) may belong only to *P. grandimana*.

Ecology

A cold water subtidal species collected at 30 m depth on the high salinity exposed coast of St. Lawrence Island, Alaska.

Genus *Cheirimedeia* J.L. Barnard

Cheirimedeia (subgenus) J.L. Barnard, 1962, p. 50; (genus) 1973, p. 22.

Type species

Protomedeia (Cheirimedeia) zotea J.L. Barnard, 1962

Additional species

There are eight known species of this genus, all of which occur in the Pacific. Four are regional (*C. macrodactyla* n. sp., *C. macrocarpa americana* n. subsp., *C. similicarpa* n. sp. and *C. zotea* J.L. Barnard). The remainder, *C. dulkeiti*[5] (Gurjanova), *C. gurjanovae*[5] (Bulytscheva), *C.*

palmata[5] (Bulytscheva) and *C. macrocarpa*[5] (Bulytscheva) occur along the Pacific coast of the U.S.S.R. Re-diagnosis of Atlantic species of *Protomedeia* in the light of the following analysis may, however, detect additional species which are more appropriately classifiable to *Cheirimedeia*.

Diagnosis

Body dorsoventrally depressed. Head lobe square, antenna 1 sinus shallow. Eye small to medium, round. Antenna 1, peduncular segment 3 shorter than segment 1; accessory flagellum multisegmented. Antenna 2 subequal to or shorter than antenna 1; flagellum 1 longer than flagellum 2. Upper lip, epistome moderately produced. Mandibular palp slender; molar with up to 2–3 raker spines. Maxilla 1 inner plate setose. Maxilla 2 lacking facial setae. Coxae shallow, increasingly so posteriorly. Coxa 1 produced forward; coxa 3 (♂) lacking stridulation ridges. Gnathopod 1, segment 5 not produced into a posterior lobe; palm distinct, dactyl usually much longer than the palm. Gnathopod 2 (♂), segment 2 lacking stridulation ridges; segment 5 subequal to or longer than segment 6 and not produced into a narrow posterior lobe; palm not incised. Peraeopods 3 and 4, anterior margin of segment 4 weakly setose (5 or less groups of setae); segment 4 anterodistally overhanging segment 5; segment 5 one third to one half the length of segment 4. Peraeopod 5 (♂), segment 2 not posterodistally notched; dactyl lacking an accessory tooth. Peraeopods 6 and 7 longer than peraeopod 5; segment 2, hind margin setose; segment 5 bearing comb spines. Pleopods, peduncles broad. Epimera not posterodistally notched, usually lacking a lateral ridge. Urosome dorsally smooth, bearing a pair of setae on segments 1 and 2. Uropod 1 bearing a peduncular spinous process; uropods 1 and 2 terminating in a group of spines; uropod 3, peduncle short, outer ramus a single segment, usually terminating in short spines and a seta; inner ramus usually half the length of the outer ramus (but subequal in *C. similicarpa*). Telson bearing a pair of apical cusps or small spines. Brood plates narrow, elliptical; setae rather sparse, not hook-tipped. Small size (regional species 4.0 to 9.0 mm).

Distribution

Known only in the north Pacific, from the U.S.S.R. and Japan in the west and from the Bering Sea to southern California in the east.

Remarks

This genus is closely related to *Protomedeia* but can be differentiated by the weaker setation and greater amount of overlap of segment 4 of peraeopods 3 and 4. In addition, antenna 2 is generally shorter than antenna 1, rather than subequal, and flagellum 2 is more pediform. The appendages of *Cheirimedeia* are generally less setose than *Protomedeia* and the body is often smaller (maximum 9.0 mm as opposed to 14.0 mm in regional species).

Barnard (1962) differentiated the genera on the basis of the amount of reduction of the third uropod inner ramus but this is not a consistent distinction (see also Discussion and Conclusions).

[5]These species clearly fall within the diagnostic characteristics of *Cheirimedeia* (see Diagnosis), and accordingly are herein transferred from *Protomedeia*.

Key to Species of Cheirimedeia of the North Pacific (Males)

1. Uropod 3, rami subequal ..... *Cheirimedeia similicarpa* n. sp. (page 39, fig. 20)
   Uropod 3, inner ramus less than two thirds the length of the outer ramus 2
2. Gnathopod 1, palm transverse, dactyl extending by half or more its length beyond the palmar defining spine 3
   Gnathopod 1, palm oblique, dactyl extending by less than half its length beyond the palmar defining spine 6
3. Gnathopod 2 similar in form to gnathopod 1, palm lacking a tooth, dactyl not overlapping; peraeopods 3 and 4, dactyl as long as segment 6; uropod 3, spines long and slender ..... *Cheirimedeia macrodactyla* n. sp. (page 38, fig. 19)
   Gnathopod 2 different in form from gnathopod 1, palm bearing a tooth, dactyl strongly overlapping; peraeopods 3 and 4, dactyl shorter than segment 6; uropod 3, spines short and stout 4
4. Gnathopod 2 defined by a tooth which fails to meet the level of the palm ..... *Cheirimedeia dulkeiti* (Gurjanova, 1951)
   Gnathopod 2 defined by a small spine at the level of the palm 5

5. Gnathopod 1, segment 6 broader than segment 5; gnathopod 2, segment 5 not broader than segment 6; uropod 3, inner ramus half the length of the outer .... *Cheirimedeia gurjanovae* (Bulytscheva, 1951)
Gnathopod 1, segment 6 narrower than segment 5; gnathopod 2, segment 5 broader than segment 6; uropod 3, inner ramus less than half the length of the outer .... *Cheirimedeia zotea* (J.L. Barnard 1962) (page 41, fig. 21)
6. Gnathopod 1, palm bearing a tooth. Gnathopod 2, palm deeply incised, defined by a large tooth ..... *Cheirimedeia palmata* (Bulytscheva, 1952)
Gnathopod 1, palm lacking a tooth. Gnathopod 2, palm not incised, defined by a small spine 7
7. Gnathopod 1, both sexes, segment 5 longer than segment 6. Gnathopod 2 (♂), segment 5 longer than segment 6, palm sinuous, defined by a spine..... ..... *Cheirimedeia macrocarpa* (Bulytscheva, 1952)
Gnathopod 1, both sexes, segment 5 equal in length to segment 6. Gnathopod 2 (♂), segment 5 subequal to segment 6, palm bearing a tooth and defined by another tooth . ..... *Cheirimedeia macrocarpa* (Bulytscheva, 1952) *americana* n. subsp. (page 36, fig. 18)

Key to the Northeastern Pacific Species of Cheirimedeia (both sexes) (Alaska to California)

1. Peraeopods 3 and 4, dactyl as long as segment 6; uropod 3 spines long and slender; gnathopod 2 (♂) similar in form to gnathopod 1, segment 5 not broader than segment 6 and narrowed into a posterior lobe; palm lacking a tooth and not overlapped by the dactyl ..... *Cheirimedeia macrodactyla* n. sp. (page 38, fig. 19)
Peraeopods 3 and 4, dactyl shorter than segment 6; uropod 3, spines short and stout; gnathopod 2 (♂) different in form from gnathopod 1, segment 5 broader than segment 6 and not narrowed into a posterior lobe; palm bearing a tooth and overlapped by the dactyl 2
2. Uropod 3, rami subequal; gnathopod 2 (♀), segment 5 broader than segment 6..... ..... *Cheirimedeia similicarpa* n. sp. (page 39, fig. 20)
Uropod 3, inner ramus half the length of the outer; gnathopod 2 (♀), segment 5 not broader than segment 6..... 3
3. Gnathopods 1 and 2 (♂, ♀), palm transverse; gnathopod 2 (♂), segment 6 distally tapered, dactyl overlapping the palm by more than half its full length..... ..... *Cheirimedeia zotea* (J.L. Barnard, 1962) (page 41, fig. 21)
Gnathopods 1 and 2 (♂, ♀), palm oblique; gnathopod 2 (♂), segment 6 not distally tapered, dactyl overlapping the palm by little more than the unguis .... *Cheirimedeia macrocarpa* (Bulytscheva, 1952) *americana* n. subsp. (page 36, fig. 18)

Cheirimedeia macrocarpa (Bulytscheva) ***americana*** n. subsp.
Figure 18

Material examined
Lelu Island, B.C. (54°12′N, 130°18′W). Bousfield 1964 stn. H13. Fine dark sand flats at low water level, bedrock and mud at mean water level. Temperature 12.0°C, salinity 18.6 °/oo. 14 July 1964. Holotype, ♂, NMC-C-1981-921; allotype, ♀, NMC-C-1981-922; paratype (NMC-C-1981-923).

Additional material
British Columbia — northern mainland: 50 specimens from Bousfield 1964 stns. H13, H43. Vancouver Island: 46 specimens from Bousfield 1977 stns. B5a, B5b, B5c (6♂♂, 4 ♀♀, 14 immatures deposited in the Smithsonian Institution (USNM)), B6b; 30 specimens from Bousfield 1964 stn. H43 (7 ♂♂, 4 ♀♀, 19 immatures deposited in the Zoological Institute, Leningrad); 1 specimen from Bousfield 1959 stn. V22; 1 specimen from Bousfield 1955 stn. F3. 6 specimens in the collection of the B.C. Provincial Museum.

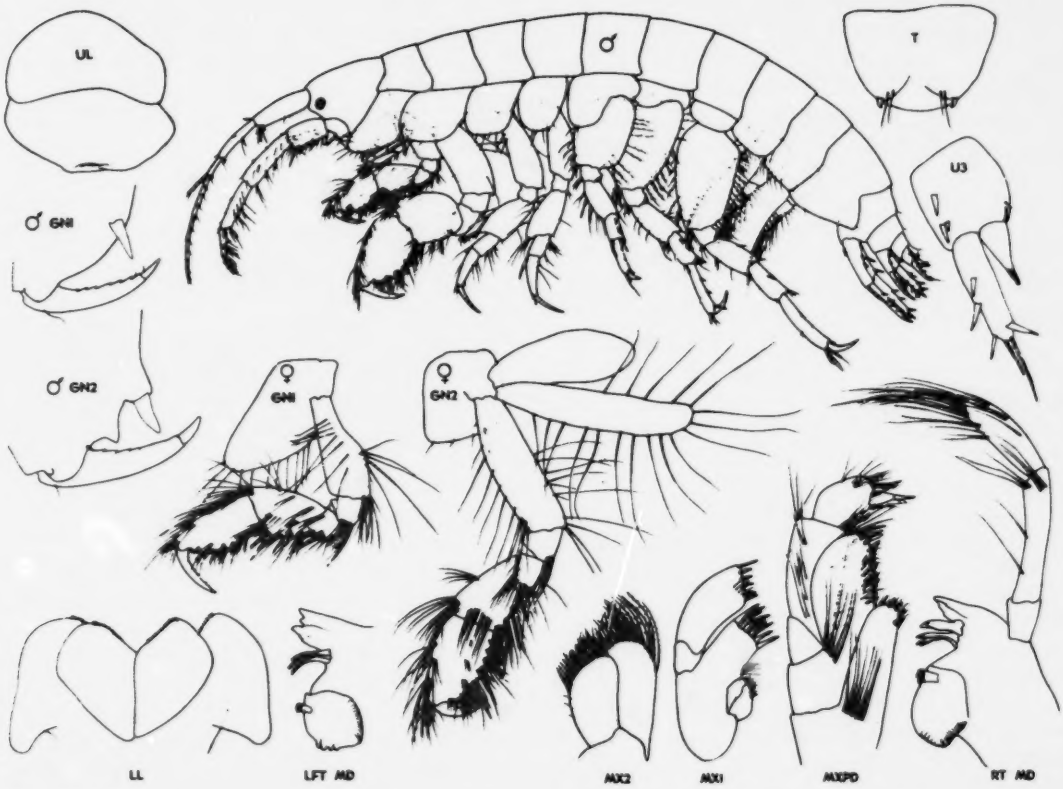


Figure 18. *Cheirimedeia macrocarpa* (Bulytscheva) *americana* n. subsp., ♂ 4.5 mm, ♀ 5.0 mm, Lelu Is., B.C.

Washington: 5 specimens from Bousfield 1966 stns. W8, W13.
Oregon: 2 specimens from Bousfield 1966 stn. W64.

Diagnosis

Holotype, male, 4.5 mm: Antenna 1 subequal to antenna 2, peduncular segment 3 less than half the length of segment 1; antenna 2 moderately setose. Maxilla 1 lacking a setal group at the base of the palp. Margins of coxae 1–5 weakly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 not longer than segment 6; segment 6, hind margin not cusped, palm oblique. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxa; segment 5 as long as but slightly wider than segment 6; segment 6 not distally tapered, hind margin not cusped, palm transverse and bearing a medial tooth and articulating defining spine; dactyl evenly curved and overlapping the palm by a quarter of its full length. Peraeopods 3 and 4, anterior margin of segment 4 barely setose, segment 4 anterodistally produced over segment 5; dactyl slightly shorter than segment 6. Peraeopod 5, coxa not deeper than coxae 1–4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus half the length of the outer, spines stout.
Size range: male to 4.5 mm.
Allotype, female, 5.0 mm: Gnathopod 2, segment 5 not broader than segment 6; palm oblique, lacking a medial tooth; dactyl not overlapping the palm. Other features similar to the male.
Size range: female 4.0 to 5.0 mm.

Distribution

Lelu Is., B.C. (54°12′N, 130°18′W) south to Netart's Bay, Tillamook Co., Oregon (45°26.5′N, 123°57′W).

Ecology

A warmer water species, occurring on brackish to full salinity sand flats at low water level on protected and semi-protected coasts. Summer temperatures recorded in the collections of

Bousfield, 1955 to 1977, were 9.0 to 16.8°C, salinities 18.6 to 33 °/oo.

Life history
Females ovigerous May to August.

Remarks
Protomedeia macrocarpa Bulytscheva 1952 differs (in both sexes) from the *americana* subspecies by the longer segment 5 of both gnathopods 1 and 2 and rather more sinuous than toothed palm of the male gnathopod 2. The distinctive antenna 2, poorly setose and strongly overlapping segment 4 of peraeopods 3 and 4, and shortened inner ramus of uropod 3 place this species clearly within *Cheirimedeia*.

Etymology
An american subspecies of the original Japan Sea species described by Bulytscheva (1952).

Cheirimedeia macrodactyla n. sp.
Figure 19

Material examined
Northeast of St. Lawrence Island, Bering Sea (64°N, 169°W). P. Slattery collection stn. 23, 7 July 1980. Holotype, ♂, NMC-C-1981-924; allotype, ♀, NMC-C-1981-925, paratypes, 1 ♀, 11 immatures, NMC-C-1981-926.

Additional material
Alaska — Bering Sea: 1 ♀, 1 immature from P. Slattery 1980 stn. 2; 1 ♂, 6 ♀♀, 11 immatures from P. Slattery 1980 stn. 23.

Diagnosis
Holotype, male, 3.0 mm: Antenna 1 slightly longer than antenna 2, peduncular segment 3 less than half the length of segment 1, antenna 2 moderately setose. Maxilla 1 lacking a setal group

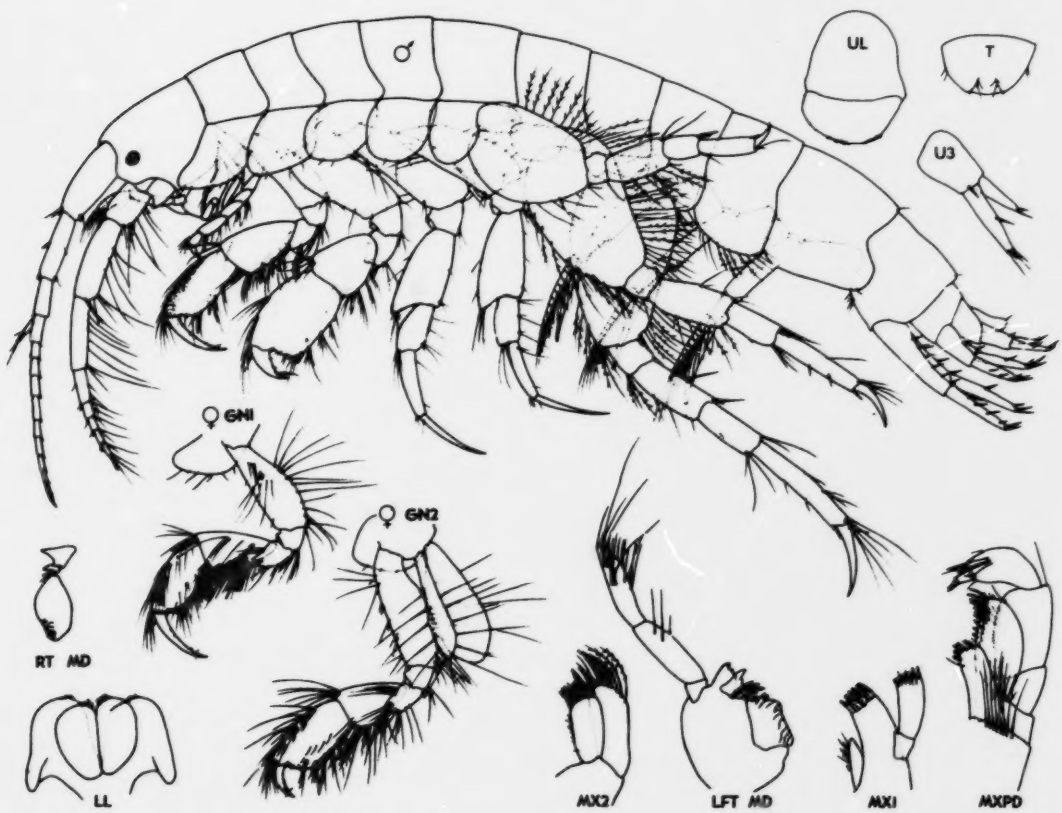


Figure 19. *Cheirimedeia macrodactyla* n. sp. ♂ 3.0 mm, ♀ 4.0 mm, St. Lawrence Is., Alaska.

at the base of the palp. Margins of coxae 1-5 weakly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 not longer than segment 6; segment 6 not distally tapered, hind margin not cusped, palm transverse. Gnathopod 2, segment 2 not anteriorly flanged, and lacking a posterior tooth at the junction of the coxa; segment 5 shorter than and as wide as segment 6; segment 6 not distally tapered, hind margin not cusped, palm transverse, lacking a medial tooth and bearing an articulating defining spine; dactyl evenly curved and not overlapping the palm. Peraeopods 3 and 4, anterior margin of segment 4 barely setose, segment 4 anterodistally produced over segment 5; dactyl longer than segment 6. Peraeopod 5, coxa not deeper than coxae 1-4; segment 2 somewhat anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus about two thirds the length of the outer, spines slender.

Size range: male 3.0 mm.

Allotype, female, 4.0 mm: Gnathopod 2, segment 5 not broader than segment 6; segment 6 not distally tapered, palm transverse but lacking a medial tubercle; dactyl not overlapping the palm. Other features similar to the male.

Size range: female 4.0 mm.

Distribution

Known only for this location.

Ecology

An exposed coast, high salinity, cold water species recorded at 30 m depth.

Life history

Females ovigerous in July.

Etymology

L.: *macro* = long, *dactyla* = nail, referring to the unusually long secretory dactyls of peraeopods 3 and 4.

Cheirimedeia similicarpa n. sp.

Figure 20

Material examined

North of Diana Island, Barkley Sound, Vancouver Island, B.C. (48°51.2'N, 125°11.6'W). Bousfield 1976 stn. B26. 21-31 m dredge over shelly mud and stones. 10°C, 32 °/oo. 8 July 1976. Holotype, ♂, NMC-C-1981-927; allotype, ♀, NMC-C-1981-928; paratypes, 21 ♂♂, 45 ♀♀, 10 immatures, NMC-C-1981-929.

Additional Material

Alaska — Bering Sea: 23 ♂♂, 20 ♀♀, 70 immatures from the collections of J. Emery and P. Slattery at St. Lawrence Island, July and August 1980 (13♂♂, 11 ♀♀, 50 immatures from P. Slattery stn. 23, Out. #1 deposited in the Smithsonian Institution (USNM); 8 ♂♂, 5 ♀♀, 15 immatures, from P. Slattery stn. 2, Dive #2, Out. #1 deposited in the Zoological Institute, Leningrad).

British Columbia: southern mainland and Vancouver Island: 23 ♂♂, 46 ♀♀, 10 immatures from Bousfield 1976 stns. B25, B26; 1 specimen from Bousfield 1975 stn. P6c; 55 specimens from the collection of C.D. Levings, 1973 and 1975.

Diagnosis

Holotype, male, 4.5 mm: Antenna 1 shorter than antenna 2, peduncular segment 3 less than half the length of segment 1; antenna 2 moderately setose. Maxilla 1 lacking a setal group at the base of the palp. Margins of coxae 1-5 weakly setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe. Segment 5 not longer than segment 6; segment 6 narrow but not distally tapered, hind margin not cusped, palm transverse. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxa; segment 5 shorter and broader than segment 6; segment 6 distally tapered, hind margin not cusped, palm transverse and bearing a medial tooth and defining spine; dactyl evenly curved and overlapping the palm by half its full length. Peraeopods 3 and 4, anterior margin of segment 4 barely setose, segment 4 anterodistally produced over segment 5; dactyl shorter than segment 6. Peraeopod 5, coxa hardly deeper than coxae 1-4; segment 2 not anteriorly bulged. Epimera lacking a lateral ridge. Uropod 3, inner ramus ¾ to subequal to the length of the outer; spines stout.

Size range: male up to 9.0 mm.

Allotype, female, 6.0 mm: Gnathopod 2, segment 5 much broader than segment 6; segment 6 not distally tapered, palm transverse, but lacking a medial tooth; dactyl overlapping the palm by 50% of its length. Other features similar to the male.

Size range: female 5.0 to 8.0 mm.

Distribution

Northeast of St. Lawrence Island, Bering Sea (64°N, 169°W), and southern B.C. mainland

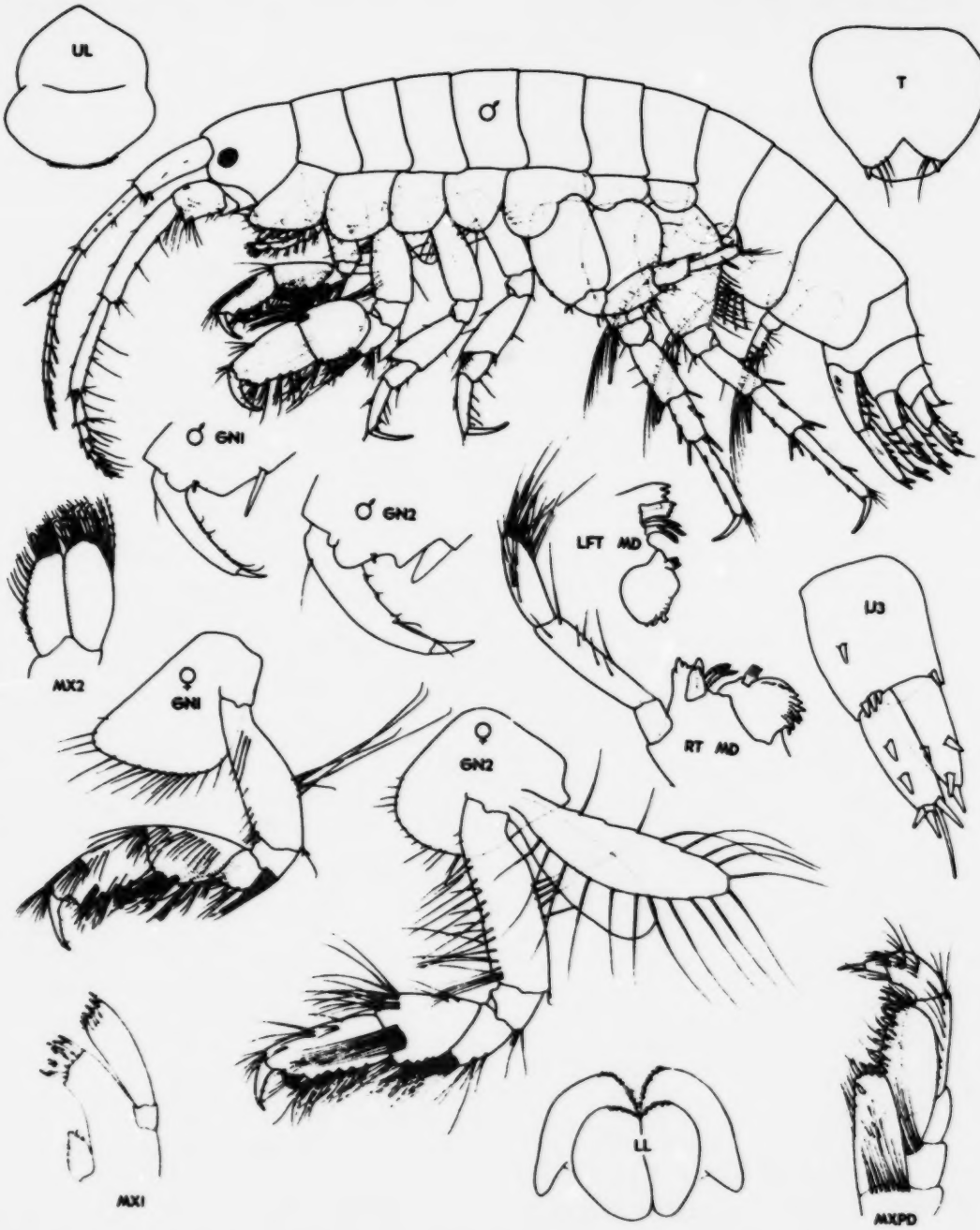


Figure 20. *Cheirimedeia similicarpa* n. sp. ♂ 4.5 mm, ♀ 6.0 mm, Diana Is., Barkley Sound, Vancouver Is., B.C.

through to southern Vancouver Island (48°51.5′N, 125°10.5′W). These two seemingly disjunct populations are morphologically identical.

Ecology
A cold-water species occurring subtidally from 21 to 67 m depth on shelly sediments in protected and semi-protected coasts. Summer temperatures and salinity recorded by Bousfield in 1976 were 10°C and 32 °/oo respectively.

Life history
Females ovigerous in July.

Etymology
L.: *similis* = similar, *carpa* = wrist, referring to the inflated condition of segment 5 which occurs in both male and female. In other Pacific species in which the male segment 5 is similarly expanded, this condition is lacking in the female.

Cheirimedeia zotea (J.L. Barnard)
Figure 21

Protomedeia (Cheirimedeia) zotea J.L. Barnard, 1962, pp. 50–52, fig. 22.

Material examined
British Columbia — southern mainland: 8 specimens from Vancouver Harbour, Trawl #2, C.D. Levings, collector. Vancouver Island — 145 specimens from Bousfield 1977 stns. B5a, B5b, B6b, B7a, B7b (8 ♂♂, 12 ♀♀, 5 immatures deposited in the Smithsonian Institution (USNM)),

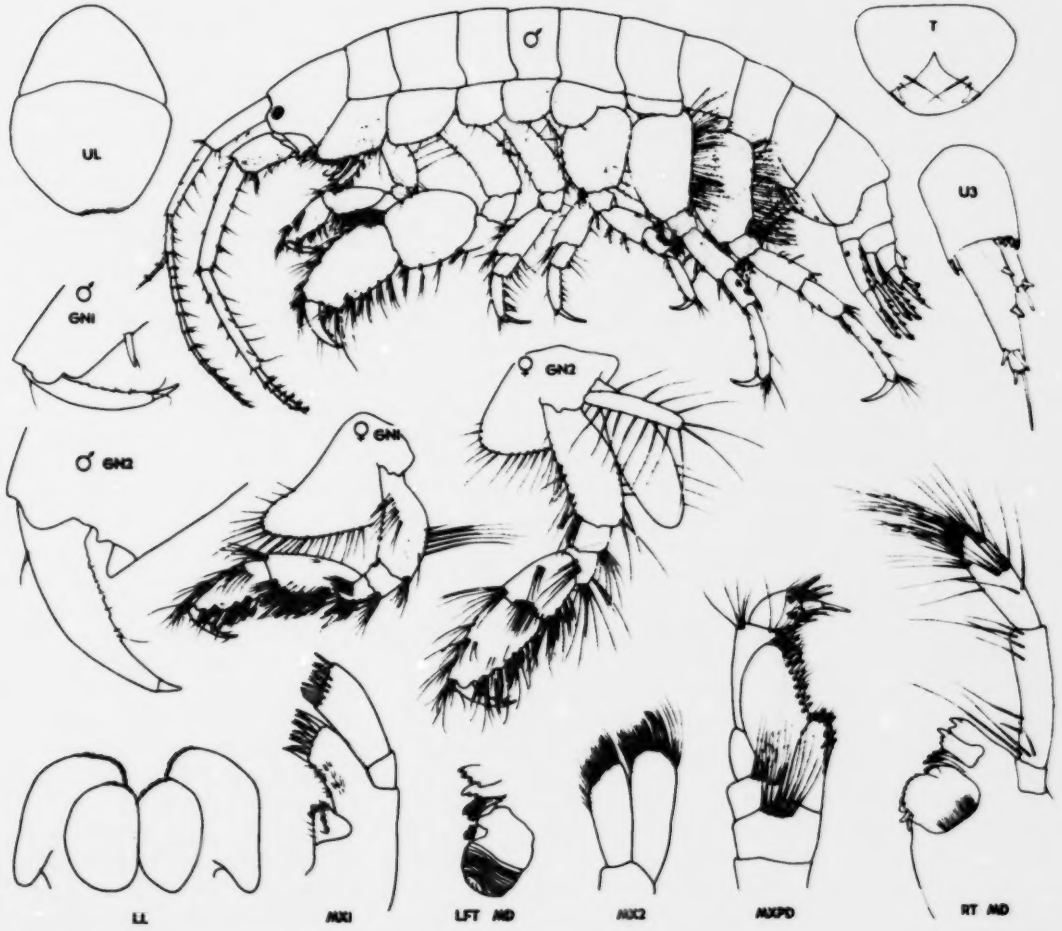


Figure 21. *Cheirimedeia zotea* (Barnard) ♂ 5.5 mm, ♀ 5.0 mm, Victoria, B.C.

B17; 15 specimens from Bousfield 1976 stns. B17, B20 (5 ♂♂, 6 ♀ ♀ deposited in the Zoological Institute Leningrad), B18, B23, B25; 28 specimens from Bousfield 1975 stns. P8, P21b; approximately 450 specimens from Bousfield 1970 stns. P716, P717; 35 specimens from Bousfield 1964 stns. H41, H43; 15 specimens from Bousfield 1959 stn. V3; 168 specimens from Bousfield 1955 stns. F3, F4, F6, F9, G13, G20; 45 specimens from the collections of G.C. Carl, J.F.L. Hart, C.D. Levings and G.W. O'Connell.

Washington: 33 specimens from Bousfield stns. W3, W30, W33, W39, W42.

Diagnosis

Male: antenna 1 slightly shorter than antenna 2, peduncular segment 3 about half the length of segment 1; antenna 2 moderately setose. Maxilla 1 lacking a setal group at the base of the palp. Margins of coxae 1–5 moderately setose. Gnathopod 1, segment 2 not posterodistally produced into a lobe; segment 5 as long as segment 6; segment 6 distally tapered, hind margin not cusped, palm transverse. Gnathopod 2, segment 2 not anteriorly flanged and lacking a posterior tooth at the junction of the coxa; segment 5 subequal to and wider than segment 6; segment 6 distally tapered, hind margin not cusped, palm transverse and bearing a medial tooth and an articulating defining spine; dactyl evenly curved and overlapping the palm by more than half its full length. Peraeopods 3 and 4, anterior margin of segment 4 barely setose, segment 4 anterodistally produced over segment 5; dactyl shorter than segment 6. Peraeopod 5, coxa somewhat deeper than coxae 3–4; segment 2 somewhat anteriorly bulged. Epimera bearing a lateral ridge. Uropod 3, inner ramus less than half the length of the outer, spines short and stout.

Female: gnathopod 2, segment 5 shorter than segment 6; segment 6 distally tapered, palm transverse, dactyl overlapping the palm by more than half its length. Other features similar to the male.

Size range: male to 5.0 mm, female 3.0 to 4.5 mm.

Distribution

Long Beach, Vancouver Island, B.C. (48°48.5′N, 125°11.0′W) south to Monterey Bay, California (37°N, 122°W)

Ecology

Exposed and moderately protected coast species occurring at low water to 113 m depth on mixed mud, sand and rock beaches. Summer temperature ranges documented in the collections of Bousfield, 1955 to 1977, were 8–17.1°C, salinities 10.4 to 33+ °/oo.

Life history

Females ovigerous in May to August.

Genus *Photis* Krøyer

Photis Krøyer, 1842, p. 155; Boeck, 1876, p. 553; Stebbing, 1888, p. 1063; Della Valle, 1893, p. 394; Sars, 1894, p. 568; Chevreux and Fage, 1925, p. 310; Barnard, 1962, p. 26; 1969a, p. 274; 1973, p. 22; Bousfield, 1973, p. 186; Lincoln, 1979, p. 516.
Eiscladus Bate and Westwood, 1863, p. 411.
Heiscladus: Norman, 1869, pp. 255, 259, 284.
Heiscladius: McIntosh, 1874, p. 269.

Type Species

Photis reinhardi Krøyer, 1842.

Additional species

There are more than 40 recognized species, ten of which occur regionally: *P. bifurcata* J.L. Barnard, *P. brevipes* Shoemaker, *P. conchicola* Alderman, *P. fischmanni* Gurjanova, *P. lacia* J.L. Barnard, *P. macinerneyi* n. sp., *P. oligochaeta* n. sp., *P. pachydactyla* n. sp., *P. parvidons* n. sp. and *P.* cf. *spasskii* Gurjanova. Fourteen additional species occur in the north Pacific: *P. nataliae* Bulytscheva, *P. kurilica* Gurjanova, *P. vinogradovi* Gurjanova, *P. strelkowi* Gurjanova, *P. baeckmannae* Gurjanova, *P. spasskii* Gurjanova, and *P. beringiensis* Tzvetkova in the U.S.S.R., and *P. spinicarpa* J.L. Barnard, *P. californica* Stout, *P. reinhardi* Krøyer, *P. macrotica* J.L. Barnard, *P. chiconola* J.L. Barnard, *P. elephantis* J.L. Barnard, and *P. viuda* J.L. Barnard in southern California.

Diagnosis

Body not dorsoventrally depressed. Head lobe acute, antennal sinus deep. Eye small to medium, round. Antenna 1, peduncular segment 3 as long as segment 1; accessory flagellum minute; flagella 1 and 2 subequal. Upper lip, epistome moderately produced. Mandibular palp quite broad; molar with up to 4 raker spines. Maxilla 1 inner plate lacking setae. Maxilla 2 bearing facial setae. Coxae deeper than

wide, lower margins often bearing dense setae, not shallowing posteriorly. Coxa 1 not produced forward; coxae 1 and 2 (♂) often shallower than coxae 3–5; coxa 3 (♂) often bearing stridulation ridges. Gnathopod 1, segment 5 produced into a posterior lobe; palm distinct, dactyl hardly longer than the palm. Gnathopod 2 (♂), segment 2 often bearing stridulation ridges; segment 5 much shorter than segment 6 and produced into a narrow posterior lobe; palm usually incised. Peraeopod 3, segment 5 less than two thirds the length of segment 4; dactyl short. Peraeopod 5 (♂), segment 2 not posterodistally notched; dactyl bearing an accessory tooth. Peraeopods 6 and 7 short, hardly longer than peraeopod 5; segment 2, hind margin not setose; segment 5 lacking comb spines. Pleopods normal. Epimera not posterodistally notched, lacking a lateral ridge. Urosome dorsally smooth, lacking setae. Uropod 1 lacking a peduncular spinous process; uropods 1 and 2 terminating in a single spine. Uropod 3, peduncle long; outer ramus bisegmented, terminating in a group of setae; inner ramus much reduced, a quarter the length of the outer. Telson bearing a pair of small apical cusps. Brood plates broad, leaf shaped; setae dense, not hook-tipped.

Distribution

A very large, cosmopolitan genus (Lincoln, 1979).

Remarks

Identification is difficult because of the variance with age in the form of the second gnathopod of the male and the slight variability between species in the female and juvenile. Female specimens differ somewhat in the intensity of setation of the coxae and the shape of gnathopods 1 and 2, but insufficient characters could be found to decisively differentiate all north Pacific species.

Key to Species of *Photis* of the North Pacific (Males)

1. Coxae 1–5, lower margins densely setose (setae closely spaced and numbering 10 or more per coxa on average) 2
   Coxae 1–5, lower margins weakly setose (setae sparse, numbering less than 10 per coxa, on average) 10
2. Gnathopod 1, palm concave or sinuous 3
   Gnathopod 1, palm oblique 9
3. Gnathopod 1, palm strongly excavate, with margin hooked downwards at the defining corner; dactyl not quite closing on the hook. Coxa 1 excavate below. Gnathopod 2, palm bearing two teeth in addition to the hind defining tooth ..... *Photis nataliae* Bulytscheva, 1952
   Gnathopod 1, palm not strongly excavate, with hind margin rounded at the defining corner; dactyl closing on the defining corner. Coxa 1 not excavate below. Gnathopod 2, palm bearing one or no teeth in addition to the hind defining tooth 4
4. Gnathopod 2 not greatly enlarged, palm lacking a tooth; dactyl evenly curved 5
   Gnathopod 2 enlarged, palm bearing a tooth; dactyl, inner margin sinuous, distally notched or medially toothed 6
5. Gnathopod 1, anterior margin of segment 5 bearing numerous spines. Gnathopod 2, segment 2, and coxa 3 lacking stridulation ridges. Peraeopods 5–7, anterior margin of segment 2 bearing long plumose setae. Known only in California ..... *Photis spinicarpa* J.L. Barnard, 1969b
   Gnathopod 1, anterior margin of segment 5 not spinose. Gnathopod 2, segment 2, and coxa 3 bearing stridulation ridges. Peraeopods 5–7, anterior margin of segment 2 bare. Known only in the Bering Sea ..... *Photis fischmanni* Gurjanova, 1955 (page 50, fig. 25)
6. Gnathopod 2, inner margin of the dactyl bearing a medial tooth 7
   Gnathopod 2, inner margin of the dactyl sinuous or distally notched but lacking a medial tooth 8
7. Gnathopod 2, palmar tooth pointed, palmar excavation narrow. Coxa 3 hardly wider than coxa 4 ..... *Photis parvidons* n. sp. (page 57, fig. 30)
   Gnathopod 2, palmar tooth square or rounded, palmar excavation broadly rounded. Coxa 3 1½ times the width of coxa 4 ..... *Photis brevipes* Shoemaker, 1942 (page 47, fig. 23)

8. Coxae 1 and 2 shallower than coxae 3 to 5. Gnathopod 1, segment 5 longer than segment 6. Coxa 3 twice the width of coxa 4. Antennae weakly to moderately setose (setae short, not longer than twice the width of the peduncle) ..... *Photis californica* Stout, 1913
Coxae 1 and 2 as deep as coxae 3 to 5. Gnathopod 1, segment 5 not longer than segment 6. Coxa 3 as wide as coxa 4. Antennae strongly setose (setae longer than twice the width of the peduncle) ..... *Photis reinhardi* Krøyer, 1842

9. Antenna 1, peduncular segments 2 and 3 twice the length of segment 1. Eyes absent. Gnathopod 1, segment 5 as long as segment 6. Gnathopod 2, segment 2 and coxa 3 lacking stridulation ridges ..... *Photis kurilica* Gurjanova, 1955
Antenna 1, peduncular segments 2 and 3 hardly longer than segment 1. Eyes present. Gnathopod 1, segment 5 shorter than segment 6. Gnathopod 2, segment 2 and coxa 3 bearing stridulation ridges ..... *Photis conchicola* J.L. Barnard, 1962 (page 49, fig. 24)

10. Gnathopod 1, palm concave or sinuous 11
Gnathopod 1, palm oblique 18

11. Gnathopod 1, segment 5 longer than segment 6. Gnathopod 2, segment 6 with a double defining tooth which is mounted on a process separate from the hand; palmar tooth lacking ..... *Photis bifurcata* J.L. Barnard, 1962, (page 46, fig. 22)
Gnathopod 1, segment 5 equal to or shorter than segment 6. Gnathopod 2, segment 6 with a single defining tooth which is attached directly to the hand; palm bearing one or two teeth 12

12. Gnathopod 1, palm strongly excavate with margin hooked downwards at the defining corner; dactyl not quite closing on the hook 13
Gnathopod 1, palm not strongly excavate, with hind margin rounded at the defining corner, dactyl closing on the defining corner 14

13. Gnathopod 2, defining tooth extending below the level of the dactyl hinge; dactyl heavy, sinuous, and extending beyond the defining tooth ..... *Photis pachydactyla* n. sp. (page 56, fig. 29)
Gnathopod 2, defining tooth not extending below the level of the dactyl hinge; dactyl not heavy, evenly curved and not reaching the defining tooth ..... *Photis vinogradovi* Gurjanova, 1951

14. Gnathopod 2, dactyl overlapping the palm 15
Gnathopod 2, dactyl not overlapping the palm 17

15. Eye large. Antennae 1 and 2 strongly setose. Gnathopod 2, palmar tooth pointed, palmar excavation conical; dactyl cusped, but not distally notched 16
Eye normal. Antennae 1 and 2 weakly setose. Gnathopod 2, palmar tooth square, palmar excavation evenly rounded; dactyl not cusped but distally notched ..... *Photis macinerneyi* n. sp. (page 54, fig. 27)

16. Dactyl, inner margin bearing a proximal tooth ..... *Photis macrotica* J.L. Barnard, 1962
Dactyl, inner margin lacking a tooth ..... *Photis chiconola* J.L. Barnard, 1962

17. Palm bearing two teeth in addition to the defining tooth ..... *Photis* cf. *spasskii* Gurjanova, 1951 (page 59, fig. 31)
Palm bearing a single small triangular tooth in addition to the defining tooth ..... *Photis strelkowi* Gurjanova, 1951

18. Gnathopod 1 simple, lacking a distinct palm. Gnathopod 2 nearly simple, lacking both palmar and defining teeth. Peraeopod 6 grossly enlarged .. *Photis elephantis* J.L. Barnard, 1962
Gnathopod 1 normally subchelate. Gnathopod 2 enlarged, palm excavate and bearing both palmar and defining teeth. Peraeopod 6 not grossly enlarged 19

19. Gnathopod 2, palm bearing two teeth in addition to the defining tooth 20
Gnathopod 2, palm bearing one tooth in addition to the defining tooth 22

20. Gnathopod 2, palm transverse, defining tooth reaching to the level of the finger hinge; dactyl distally notched ..... *Photis baeckmannae* Gurjanova, 1938
Gnathopod 2, palm oblique, defining tooth not reaching to the level of the finger hinge; dactyl not distally notched 21

21. Gnathopod 1, segment 5, posterior lobe narrow, less than half the length of the anterior margin. Gnathopod 2, segment 2 and coxa 3 lacking stridulation ridges. Known only in the Bering Sea ..... *Photis spasskii* Gurjanova, 1951
22. Gnathopod 2, defining tooth produced below the level of the dactyl hinge ..... *Photis oligochaeta* n. sp. (page 54, fig. 28)
Gnathopod 2, defining tooth not produced below the level of the dactyl hinge 23
23. Antennae 1 and 2 subequal, weakly setose. Gnathopod 2, palmar tooth square; dactyl, inner margin slightly sinuous, notched distally. Known only south of central B.C. ..... *Photis lacia* J.L. Barnard, 1962 (page 52, fig. 26)
Antenna 1 longer than 2, both strongly setose. Gnathopod 2, palmar tooth pointed; dactyl evenly convex. Known only in the Bering Sea ..... *Photis beringiensis* Tzvetkova, 1980

Key to Species of *Photis* of the North Pacific[6] (Females)

1. Coxae 1–5, lower margins densely setose (setae closely spaced and numbering more than 10–15 per coxa on average) 2
Coxae 1–5, lower margins weakly setose (setae sparse, numbering less than 10–15 per coxa on average) 9
2. Gnathopod 1, palm concave or sinuous 3
Gnathopod 1, palm oblique 5
3. Coxa 1, anterior margin convex, produced to a distal point. Gnathopod 1, segment 5, posterior lobe broad, more than half the length of the anterior margin. Peraeopods 5–7, anterior margins bearing long plumose setae ..... *Photis spinicarpa* J.L. Barnard, 1969b
Coxa 1, anterior margin straight, evenly rounded distally. Gnathopod 1, segment 5, posterior lobe narrow, less than half the length of the anterior margin. Peraeopods 5–7, anterior margins bare 4
4. Antennae 1 and 2 strongly setose. Gnathopod 1, palm sinuous and hardly excavate ..... *Photis reinhardi* Krøyer, 1842
Antennae 1 and 2 moderately setose. Gnathopod 1, palm strongly excavate ..... *Photis parvidons* n. sp. (page 57 and fig. 30)
5. Eyes lacking ..... *Photis kurilica* Gurjanova, 1955
Eyes present 6
6. Gnathopod 2, palm oblique 7
Gnathopod 2, palm concave or sinuous 8
7. Gnathopod 2 bearing an obturator spine, dactyl reaching the length of the palm; segment 2 and coxa 3 lacking stridulation ridges. Known only in California ..... *Photis conchicola* J.L. Barnard, 1962 (page 49, fig. 24)
Gnathopod 2 lacking an obturator spine, dactyl not reaching the length of the palm; segment 2 and coxa 3 bearing stridulation ridges. Known only in Alaska ..... *Photis fischmanni* Gurjanova, 1955 (page 50, fig. 25)
8. Gnathopod 1, segment 5, posterior lobe two-thirds the length of the anterior margin. Gnathopod 2, segment 2 produced into an anterodistal lobe ..... *Photis californica* Stout, 1913
Gnathopod 1, segment 5, posterior lobe half the length of the anterior margin. Gnathopod 2, segment 2 not produced into an anterodistal lobe ..... *Photis brevipes* Shoemaker, 1942 (page 47, fig. 23)
9. Gnathopod 2, palm concave or sinuous 10
Gnathopod 2, palm oblique 15
10. Gnathopod 2, palm bearing a tooth; dactyl shorter than the length of the palm ..... *Photis vinogradovi* Gurjanova, 1951
Gnathopod 2, palm lacking a tooth; dactyl reaching the length of the palm 11

[6] Insufficient information available for *Photis nataliae, P. beringiensis* and *P. elephantis*

11. Coxae 1–5, lower margins bearing more than 5 setae on average. Eye large for the genus ..... *Photis macrotica* J.L. Barnard, 1962
Coxae 1–5, lower margins bearing fewer than 5 setae, on average. Eye normal ..... *Photis viuda* J.L. Barnard, 1962
12. Antennae 1 and 2 subequal in length. Eye larger than the entire head lobe ..... *Photis chiconola* J.L. Barnard, 1962
Antenna 1 shorter than 2. Eye not larger than the entire head lobe 13
13. Gnathopod 1, segment 5, posterior lobe more than half the length of the anterior margin ..... *Photis bifurcata* J.L. Barnard 1962, (page 46, fig. 22)
Gnathopod 1, segment 5, posterior lobe less than or equal to half the length of the anterior margin 14
14. Gnathopod 1, posterior margin of segment 6 abruptly angled to define the palm, obturator spine lacking. Gnathopod 2, segment 5 two thirds the length of segment 6 ..... *Photis spasskii* Gurjanova, 1951
Gnathopod 1, posterior margin of segment 6 evenly curved, obturator spine present. Gnathopod 2, segment 5 half the length of segment 6 ..... *Photis pachydactyla* n. sp. (page 56, fig. 29)
15. Gnathopod 1, segment 5, posterior lobe less than half the length of the anterior margin 16
Gnathopod 1, segment 5, posterior lobe half or more than the length of the anterior margin 17
16. Antennae 1 and 2 weakly setose, setae hardly longer than the width of the peduncle. Known only south of central B.C. ..... *Photis macinerneyi* n. sp. (page 54, fig. 27)
Antennae 1 and 2 moderately setose, setae 2 to 3 times longer than the width of the peduncle. Known only north of central B.C. ..... *Photis* cf. *spasskii* Gurjanova, 1951 (page 59, Fig. 31)
17. Gnathopod 2, segment 2 anterodistally lobed ..... *Photis baeckmannae* Gurjanova, 1938
Gnathopod 2, segment 2 not anterodistally lobed 18
18. Gnathopods 1 and 2, segment 6 very slender, palm not demarcated by a change of angle ..... *Photis oligochaeta* n. sp. (page 54, fig. 28)
Gnathopods 1 and 2, segment 6 triangular in shape, palm demarcated by a change of angle 19
19. Gnathopod 1, segment 5 as long as segment 6. Known only south of central B.C. ..... *Photis lacia* Barnard, 1962 (page 52, fig 26)
Gnathopod 1, segment 5 shorter than segment 6. Known only in the U.S.S.R ..... *Photis strelkowi* Gurjanova, 1951

Photis bifurcata J.L. Barnard
Figure 22

Photis bifurcata J.L. Barnard, 1962, pp. 30–31, fig. 10; 1964, p. 240.

Material examined

Alaska — southeastern coast: 1 ♀, 1 immature from Bousfield 1980 stn S7B1; 2♂♂ from Bousfield 1961 stns. A6, A171–2.

British Columbia — Queen Charlotte Islands: 1 ♂, 1 ♀, 2 immatures from NMC acc. no. 68–155, Island Bay; northern mainland: 4 ♂♂, 8 ♀♀, 9 immatures from Bousfield 1964 stns H12, H33, H47, H49, H53; southern mainland and Vancouver Island: 24 ♂♂, 62 ♀♀ from Bousfield 1977 stns. B1 (7 ♂♂, 11 ♀♀ deposited in the Zoological Institute, Leningrad), B6a, B12c; approximately 300 specimens from Bousfield 1976 stns. B7, B27; 69 ♂♂, 62 ♀♀ from Bousfield 1975 stns. P5a, P5b, P5c, P17d, (1 ♂, 2 ♀♀ deposited in the Smithsonian Institution (USNM)); 7 ♂♂ from Bousfield 1970 stn P719; 5 ♂♂, 4 ♀♀, 4 immatures from Bousfield 1955 stns. F1, P4, P5, P7; 5 ♂♂, 7 ♀♀, 1 immature from the collections of G.C. Carl, J.F.L. Hart, C. Haylock and N.A. Powell.

Washington: 6 ♂♂, 15 ♀♀, 7 immatures from Bousfield 1966 stns. W34, W40, W42, W47.

Oregon: 2 ♂♂, 4 ♀♀ from Bousfield 1966 stns. W57, W58.

Diagnosis

Male: eye small; antennae 1 and 2 weakly setose; antenna 2 peduncular segment 4 anteriorly inflated; coxae, lower margins weakly setose; coxae 1 and 2 not shallower than coxae 3–5, lower margins rounded; gnathopod 1, segment 5 much longer than segment 6, posterior lobe shallow and more than half the length of the anterior margin;

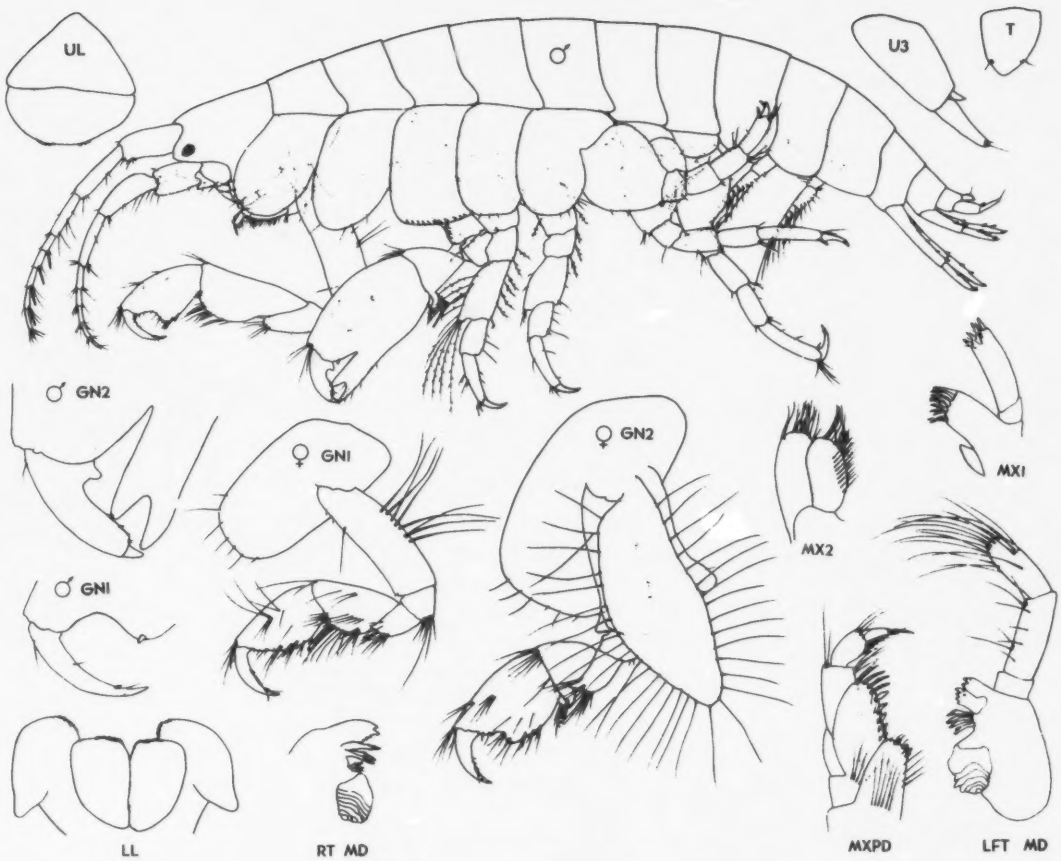


Figure 22. *Photis bifurcata* Barnard ♂ 3.5 mm, ♀ 3.5 mm, Trial Island Point, Victoria, B.C.

segment 6 narrow, palm concave; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a bifid defining tooth which reaches beyond the theoretical depth of the palm as defined by the anterodistal margin of the segment; palmar excavation narrow, hinge tooth lacking; dactyl, inner margin sinuous, with a proximal bump and distal swelling; dactyl scarcely overlapping the palm; coxa 3, lower margin bearing stridulation ridges.

Female: gnathopod 1, segment 5, posterior lobe more than half the length of the anterior margin; segment 6, palm convex; gnathopod 2, palm concave; gnathopod 2 and coxa 3 lacking stridulation ridges. Other features similar to the male.

Size range: male to 4.0 mm, female 2.0 to 3.5 mm.

Pigmentation: dorsum of segment 5 dark banded.

Distribution

Chichagof Island, Alaska (57°47′N, 136°18′W) south to Bahia de San Cristóbal, Baja California (27°N, 115°W).

Ecology

Occurs on bedrock, sand and sandy mud on exposed and semi-protected coasts at low water level to a depth of 60 m. Temperatures recorded in the collections of Bousfield, 1955–1980, were 10–17.9°C, salinities 28–34 °/oo.

Life history

Females ovigerous from May to August.

Photis brevipes Shoemaker, 1942
Figure 23

Photis brevipes Shoemaker, 1942, pp. 25–27, fig. 9; J.L. Barnard, 1962, pp. 31–33, fig. 11; 1964, pp. 240–241; 1969b, pp. 148–151.
Photis californica: J.L. Barnard, 1954, pp. 26–27, pls. 23, 24 (not Stout, 1913)

Material examined

Alaska — southeastern coast: 75 specimens from Bousfield 1980 stns. S5B1, S8B1, S11B1, S18F1,

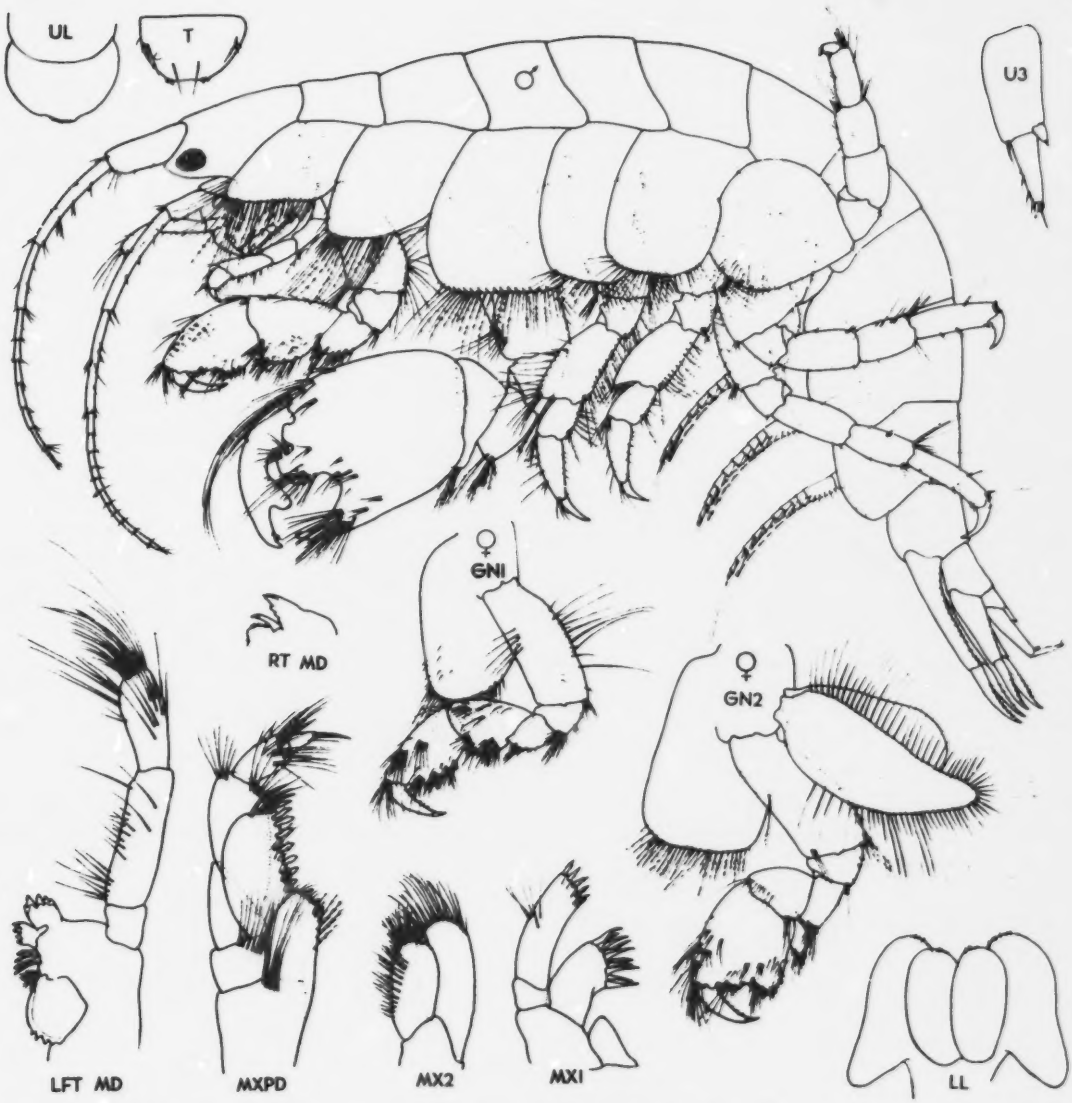


Figure 23. *Photis brevipes* Shoemaker ♂ 4.5 mm, ♀ 3.5 mm, Departure Bay, Nanaimo, B.C.

S18F2 (9 ♂♂, 13 ♀ ♀, 18 immatures deposited in the Zoological Institute, Leningrad), S18F3 (5 ♂♂, 2 ♀ ♀, 4 immatures deposited in the Smithsonian Institution (USNM)), S23F1; 75 specimens from Bousfield 1961 stns. A3, A6, A75, A80, A96, A151, A153, A167, A168, A171–2, A175.

British Columbia: Queen Charlotte Islands: 155 specimens from Bousfield 1957 stns. H2, H2a, H3, H5, H8b, H11, H14, E14a, E14b, E25, W3a, W8, N2. Northern mainland: approximately 400 specimens from Bousfield 1964 stns. H1, H5, H8, H12, H21, H23, H25, H26, H29, H30, H31, H33, H36, H37, H39, H47, H48, H50, H53, H57, H58, H65. Southern mainland and Vancouver Island: approximately 400 specimens from Bousfield 1977 stns. B1, B2, B3, B5a, B6a, B6b, B7a, B11b, B13, B14, B15, B17, E1, E2, E4, P5; approximately 120 specimens from Bousfield 1976 stns. B4, B5, B7, B18, B20, B23, B25, B26, B27, B28; approximately 550 specimens from Bousfield 1975 stns. P3a, P3b, P5a, P5b, P5c, P5d, P8, P11, P12, P13, P14a, P17a, P17d, P20, P21a, P29a, P29b, P29c; approximately 1750 specimens from Bousfield 1970 stns. P701, P702, P710b, P711, P712, P714,

P715, P716, P718, P719; approximately 275 specimens from Bousfield 1964 stns. H43, H44; approximately 550 specimens from Bousfield 1959 stns. V3, V4b, V5, V17, V18, V22, V27, O1, O2b, O5, O6, O7b, O7d, O11, O13, N1, N11, N22; approximately 200 specimens from Bousfield 1955 stns. F1, F3, F6, F9, G2, G4, G15, P2, P6a, P6c, P7, P9; approximately 650 specimens from the collections of G.C. Carl, K.E. Conlan, S. Cross, D.V. Ellis, the Fisheries Research Board at Nanaimo, J.M. Green, J.F.L. Hart, C. Haylock, M. Haylock, D. Kittle, R.K. Lee, C.D. Levings, C. Lobban, P. O'Rourke, N.A. Powell, J.W. Scoggan, W. Spreadborough and C.H. Young.
Washington: approximately 550 specimens from Bousfield 1966 stns. W7, W8, W13, W15, W22, W30, W34, W35, W39, W40.
Oregon: approximately 300 specimens from Bousfield 1966 stn. W64.

Diagnosis
Male: eye medium; antennae 1 and 2 moderately setose; antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins densely setose; coxae 1 and 2 shallower than coxae 3–5, lower margins parallel with the body mid-line; gnathopod 1, segment 5 subequal to 6, posterior lobe shallow, more than half the length of the anterior margin; segment 6, palm concave; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a single large defining tooth which extends to the depth of the palm; palmar excavation broadly rounded or square; palmar hinge tooth square or rounded; dactyl convex, not overlapping the palm, bearing centrally a large triangular protuberance which fits into the palmar indentation in aposition to the hinge tooth, and distally a cusp at the junction of the unguis; coxa 3, lower margin bearing stridulation ridges.
Female: coxae 1 and 2 same depth as 3–5; gnathopod 1, segment 5, posterior lobe more than half the length of the anterior margin; palm convex; gnathopod 2, palm sinuous, slightly excavate; gnathopod 2 and coxa 3 lacking stridulation ridges; other features similar to the male.
Juvenile male: gnathopod 2, hinge tooth pointed and more proximal to the palmar defining tooth, causing the palmar indentation to be narrow; dactyl protuberance more distal than in the adult, but present in juveniles of at least 3 mm length.
Size range: male to 7.0 mm; female ovigerous at 2.5 to 6.0 mm.
Pigmentation: dark bands on segments 1, 5 and 7.

Distribution
Widely ranging from southeastern Alaska (Prince William Sound, 60°46′N, 146°31′W) south to Bahia Magdalena, Baja California (26°42′30″N, 113°34′15″W).

Ecology
Occurs in generally high salinity protected and exposed coasts predominately on sandy sediments at low water level to 135 m depth. Temperature ranges recorded in the collections of Bousfield, 1955–1980, were 8 to 15.7°C, salinities 14.8 to 33.4 °/oo.

Life history
Females ovigerous from May to November.

Remarks
Immature specimens cannot be differentiated from *P. parvidons*. In the young male *P. brevipes*, the gnathopod 2 palmar tooth and excavation are narrower, approximating the gnathopod 2 of *P. parvidons*. In the subadult female *P. parvidons*, gnathopod 1 is oblique as in *P. brevipes*.

Photis conchicola Alderman?
Figure 24

Photis conchicola Alderman, 1936, pp. 66–67, figs. 39–43; Barnard, 1962, pp. 36–39, figs. 14, 15.

Material examined
Washington: one ♂ from Bousfield 1966 stn. W40, Mukkaw Bay at Sooes Pt., Clallam Co. (48°19′N, 124°40′W), 31 July 1966. Fine sand, shelly sand, soft sandstone, bedrock and boulders; kelp, *Phyllospadix, Zostera, Chorda*. Low water to mean water levels.

Diagnosis
Male: eye medium; antennae 1 and 2 strongly setose, antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins strongly setose; coxae 1 and 2 shallower than coxae 3–5, lower margins straight, parallel with the body midline; gnathopod 1, segment 5 shorter than segment 6, posterior lobe broad, more than half the length of the anterior margin; segment 6 rather narrow, palm oblique; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a single heavy defining tooth which extends beyond the

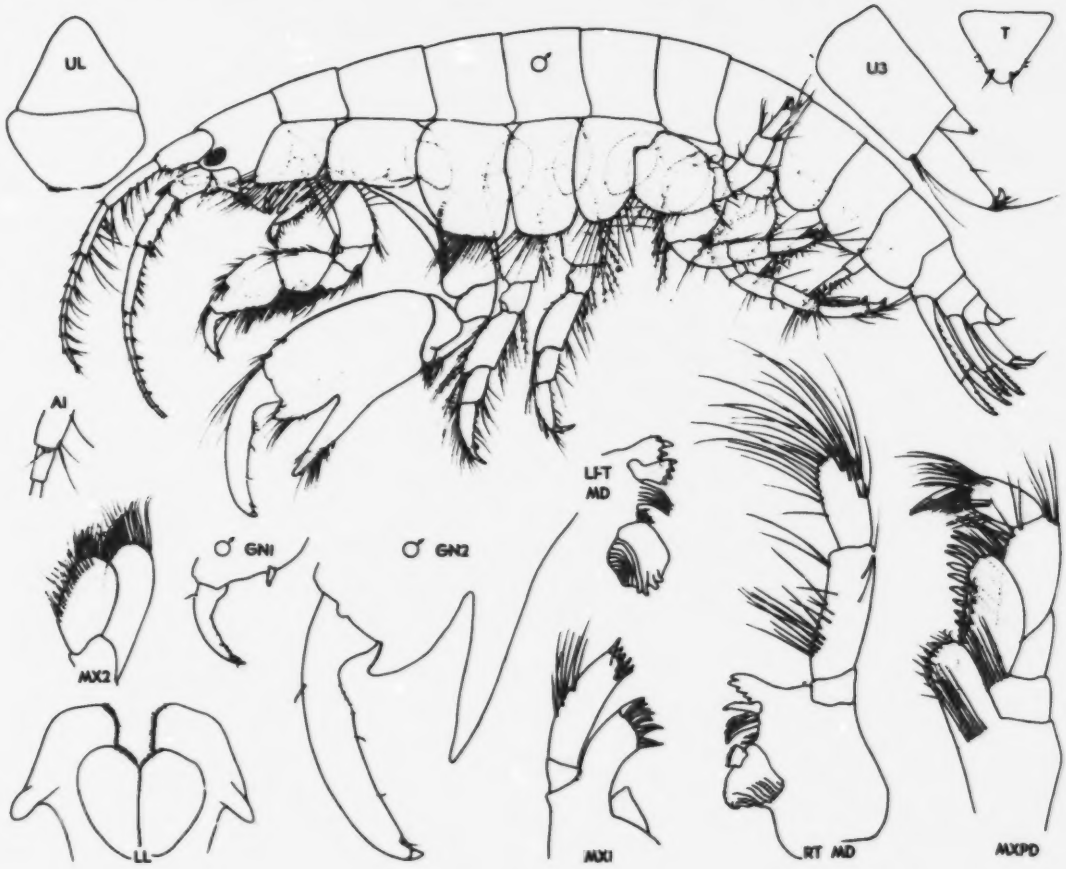


Figure 24. *Photis conchicola* Alderman ♂ 5.5 mm, Mukkaw Bay at Sooes Pt., Clallam Co., Washington.

theoretical depth of the palm as defined by the anterodistal margin of the segment; palmar excavation conical, palmar hinge tooth pointed; dactyl heavy, overlapping the palm, inner margin sinuous, bearing a small cusp at the unguis and a shallow medial inflation; coxa 3, lower margin bearing stridulation ridges.

Size range: male, 5.5 mm; female unknown in Washington, 3.2 mm in the California material of Barnard (1962).

Distribution

Mukkaw Bay, Washington (48°19′N, 124°40′W) (?) south to La Jolla, California (32°52′N, 117°16′W).

Ecology

A warmer water species, occurring on exposed coasts in the intertidal and rarely subtidally to 42 m. Temperature recorded at the Washington station was 12.3°C, salinity 32.6 °/oo.

Remarks

The specimen described herein is considerably larger than the largest males of *P. conchicola* described by Barnard (1962) (5.5 mm as compared to 3.7 mm, respectively) and therefore could be either a local variant or a postmature. It differs only in the form of the second gnathopod, whereby the defining and hinge teeth are longer and more widely separated and the dactyl is longer and more sinuous.

Photis fischmanni Gurjanova
Figure 25

Photis fischmanni Gurjanova, 1938, pp. 849–851, fig. 595.

Material examined

4 ♂♂, 40 ♀♀, approximately 300 immatures from northeast of St. Lawrence Island, Bering Sea

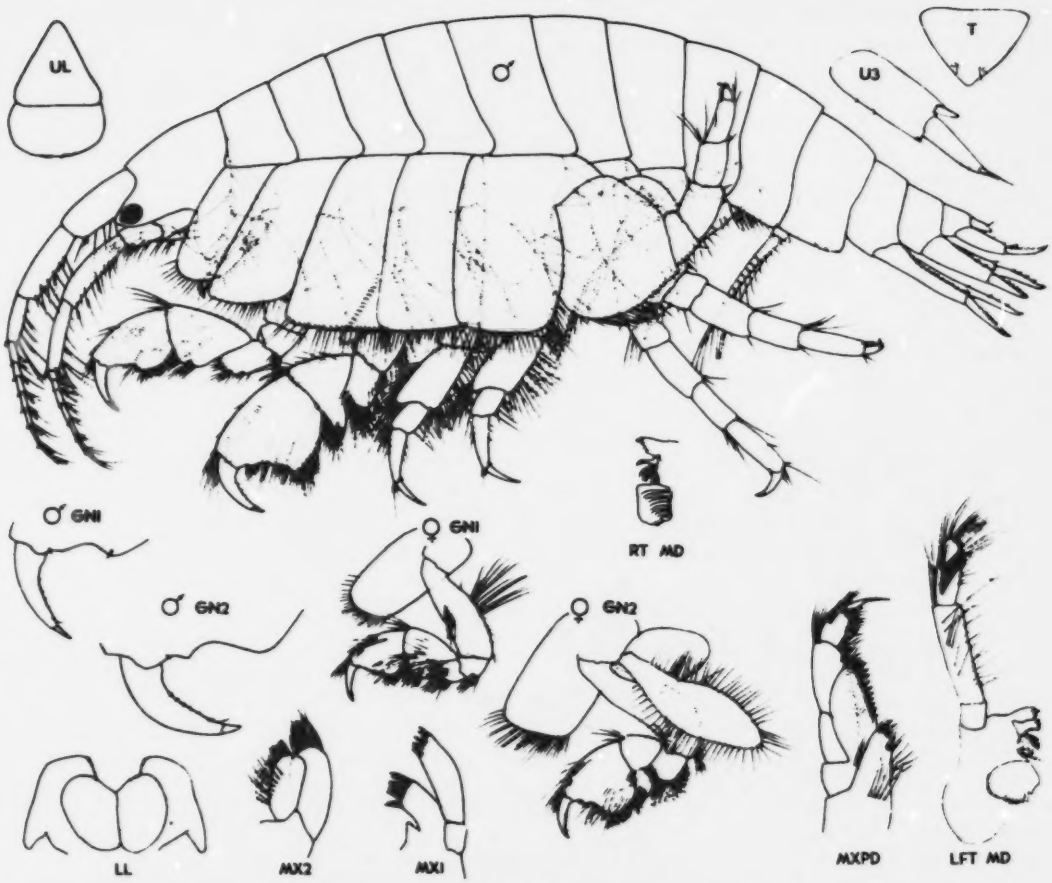


Figure 25. *Photis fischmanni* Gurjanova ♂ 5.5 mm, ♀ 6.0 mm, St. Lawrence Is., Alaska.

(64°N, 169°W). J. Emery collection, 1 Aug. 1980 and P. Slattery collection, 1–10 July 1980. 1 ♂, 1 ♀, 24 immatures from P. Slattery Dive #2, Out #3 (NMC acc. no. 1980–554) deposited in the Smithsonian Institution (USNM); 1 ♂, 1 ♀ from P. Slattery Stn. 5 (NMC acc. no. 1980–554) deposited in the Zoological Institute, Leningrad.

Diagnosis

Male: eye medium, antennae 1 and 2 strongly setose, antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins strongly setose; coxae 1 and 2 hardly shallower than coxae 3–5, with coxa 2 intermediate in depth between 1 and 3, lower margins straight, parallel with the body mid-line; gnathopod 1, segment 5 longer than segment 6, the posterior lobe fairly broad, about half the length of the anterior margin; segment 6 fairly broad, palm slightly concave; gnathopod 2, segment 2 bearing stridulation ridges and anterodistally produced into a strong lobe; segment 6 similar in form to gnathopod 1, lacking palmar teeth, palm slightly excavate; dactyl evenly convex and not overlapping the palm; inner margin strongly cusped but lacking a protuberance; coxa 3, lower margin bearing stridulation ridges.

Female: gnathopod 1, segment 5 as long as segment 6, posterior lobe about half the length of the anterior margin; segment 6, palm convex but slightly sinuous; gnathopod 2, segment 6, palm broader but similarly convex and slightly sinuous; gnathopod 2 and coxa 3 bearing stridulation ridges; other features similar to the male.

Size range: male to 5.5 mm, female 5.0 to 6.0 mm.

Distribution

Bering Sea, off St. Lawrence Island, Alaska (64°N, 169°W); off Kamchatka, U.S.S.R. (55°N, 165°E); Chukchi Sea (70°N, 170°W); Kurile Islands, U.S.S.R. (45°N, 150°E).

Ecology
An Arctic species occurring subtidally at 7.5 to 37.5 m depth.

Life history
No females ovigerous when collected in July and August, although brood plates were present.

Photis lacia J.L. Barnard
Figure 26

Photis lacia Barnard, 1962, pp. 42–44, fig. 18.

Material examined
British Columbia — northern mainland: 7 specimens from Bousfield 1964 stn. H49; Vancouver Island: approximately 300 specimens from Bousfield 1976 stns. B9e, B10b, B10d, B26, B27 (representative specimens deposited in the Smithsonian Institution and the Zoological Institute, Leningrad); 4 specimens from Bousfield 1975 stns. P13, P21a.

Diagnosis
Male: eye small; antennae 1 and 2 weakly setose; antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins weakly setose, coxae 1 and 2 shallower than coxae 3–5, coxa 2 intermediate in depth between 1 and 3; lower margins of coxae 1 and 2 rounded, hind margin of coxa 2 concave; gnathopod 1, segment 5 subequal to segment 6, posterior lobe shallow, more than half the length of the anterior margin; segment 6 narrow, palm convex; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a single narrow defining tooth which does not reach to the depth of the palm; palmar excavation subconical; palmar hinge tooth flat, square; dactyl convex, inner margin sinuous, bearing a

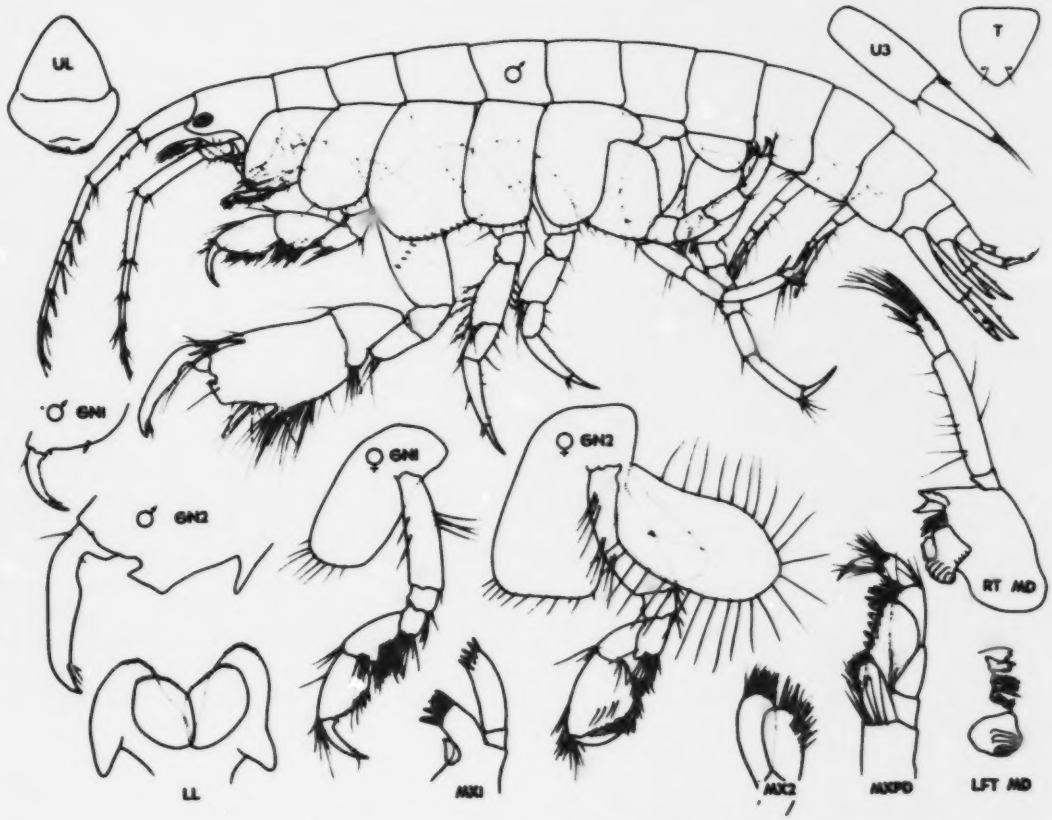


Figure 26. *Photis lacia* J.L. Barnard ♂ 3.0 mm, ♀ 3.3 mm, Trevor Channel, Barkley Sound, Vancouver Is., B.C.

cusp at the junction of the unguis but lacking a protuberance; dactyl scarcely overlapping the palm; coxa 3, lower margin bearing stridulation ridges.

Female: coxae 1 and 2 subequal to coxae 3–5; gnathopod 1, segment 5, posterior lobe more than half the length of the anterior margin; palm convex; gnathopod 2, palm convex; gnathopod 2 and coxa 3 lacking stridulation ridges; other features similar to the male.

Size range: male to 3.0 mm; female to 3.3 mm.

Distribution

Goose Island, B.C. (51°56′N, 128°26′W) south to Pt. Conception, California (34°26.40′N, 120°21.45′W).

Ecology

Occurs subtidally from 7.2 to 39.6 m in sandy sediments on exposed coasts. Temperatures recorded in the collections of Bousfield, 1964–1976, were 8–12°C, salinities 32–33+ °/oo.

Life history

Females ovigerous in June and July.

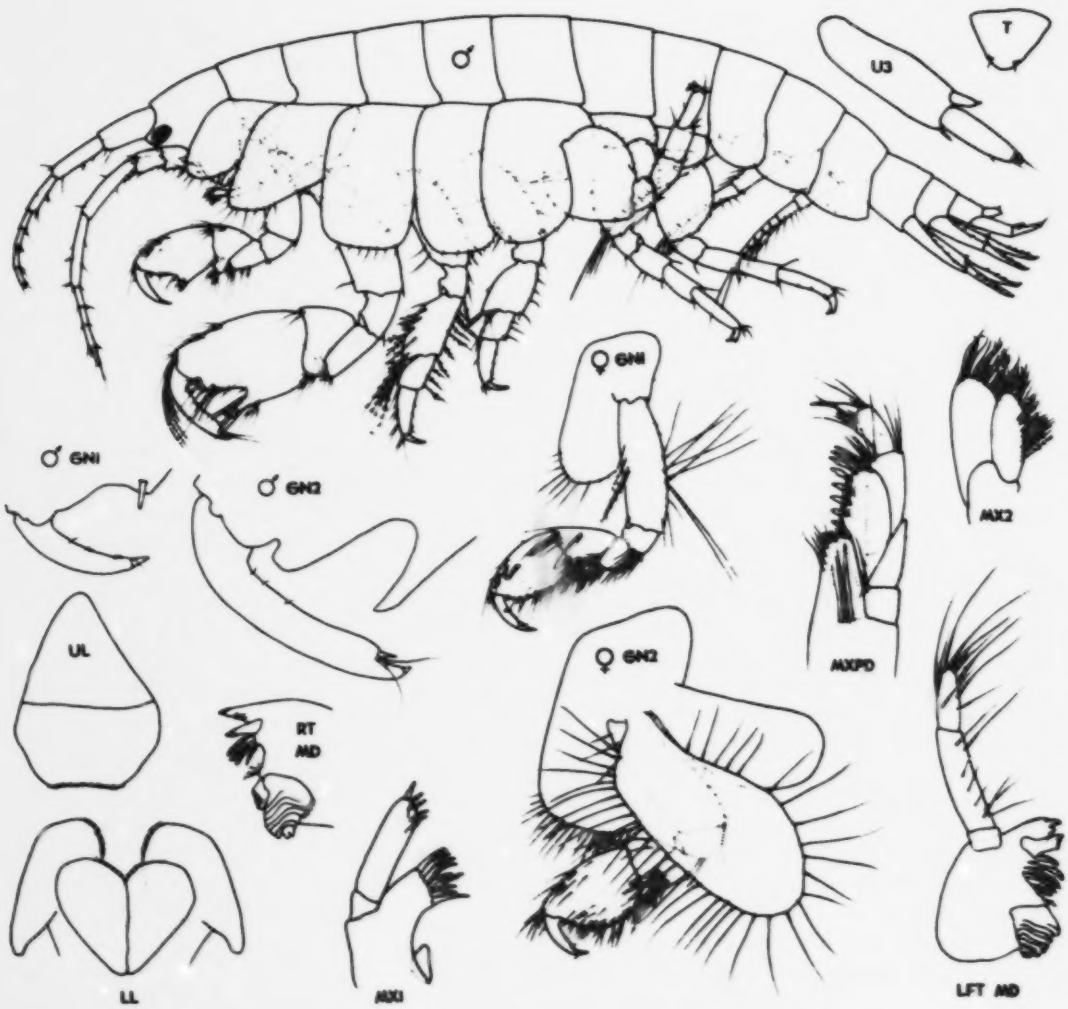


Figure 27. *Photis macinerneyi* n. sp. ♂ 4.3 mm, ♀ 4.0 mm, Witty's Lagoon, Victoria, B.C.

Photis macinerneyi n. sp.
Figure 27

Material examined
Witty's Lagoon, Victoria, B.C. (48°22'N, 123°31'W), Bousfield 1977 stn. B5a, 17 May 1977. Subtidal dredge over dark organic ripple sand. Temperature 9°C, salinity 33°/oo. Holotype, ♂, NMC-C-1981-933, allotype, ♀, NMC-C-1981-934; paratypes, 1 ♂, 2 ♀♀, NMC-C-1981-935.

Additional material
British Columbia — Vancouver Island: approximately 50 ♂♂ and 60 ♀♀ from Bousfield 1977 stns. B1, B5a, B6b, B18; 13 ♂♂, 11 ♀♀, 12 immatures from Bousfield 1976 stns. B9c, B11b; 7 ♂♂, 15 ♀♀, 2 immatures from Bousfield 1975 stns. P21b (3 ♂♂, 3 ♀♀ deposited in the Zoological Institute, Leningrad), P22, P29a, P29c; 2 ♂♂, 3 ♀♀, 2 immatures deposited in the Smithsonian Institution (USNM)), 4 ♂♂, 4 ♀♀ from Bousfield 1970 stns. P716, P717, 1 immature from Bousfield 1959 stn. V7; 1 ♂ from Bousfield 1955 stn. F3.
Washington: 5 ♂♂, 7 ♀♀ from Bousfield 1966 stns. W8, W39.

Diagnosis
Holotype, male, 4.3 mm: Eye medium; antennae 1 and 2 weakly setose, antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins weakly setose; coxae 1 and 2 shallower than coxae 3–5, coxa 2 intermediate in depth between 1 and 3, lower margins of coxae 1 and 2 rounded; gnathopod 1, segment 5 shorter than segment 6, posterior lobe narrow, less than half the length of the anterior margin; segment 6, palm concave; gnathopod 2, segment 2 lacking stridulation ridges; segment 6 with a single defining tooth which reaches to the theoretical depth of the palm as defined by the anterodistal margin of the segment; palmar excavation broadly rounded, hinge tooth square; dactyl overlapping the palm, inner margin strongly notched distally, but otherwise evenly convex and lacking a protuberance; coxa 3, lower margin lacking stridulation ridges.
Size range: male to 4.3 mm.
Allotype, female, 4.0 mm: Gnathopod 1, segment 5 shorter than segment 6, posterior lobe narrow, less than half the length of the anterior margin; segment 6, palm convex; gnathopod 2, palm convex; other features similar to the male.
Size range: female 2.3 to 4.0 mm.

Distribution
Lady Ellen Point, Broughton Strait, Vancouver Island (50°36'N, 127°07'W) south to Neah Bay, Clallam County, Washington (48°22'N, 124°36'W)

Ecology
Occurs over sandy substrates at low water level to 45 m depth on exposed and protected coasts. Temperatures recorded in the collections of Bousfield, 1955–1977, were 9–14.8°C, salinities 30.5–33+ °/oo.

Life history
Females ovigerous from May to August.

Remarks
The second gnathopod of this species is similar to that of *P. lacia*, but differs in that the defining tooth extends to the depth of the palm and the palmar excavation is rounded, rather than conical. In addition, the palm of gnathopod 1 is concave rather than convex. This species also resembles *P. conchicola* in the form of the second gnathopod but differs in the weaker setation of antennae and coxae, concavity of the palm of the male gnathopod 1 and convexity of the female gnathopod 2, absence of stridulation ridges, narrower lobation of gnathopod 1, segment 5, and shape of the first two male coxae.

Etymology
This species is named in honour of Dr. J.E. McInerney, former director of the Bamfield Marine Station, where much of the field research on the exposed coast of Vancouver Island was conducted.

Photis oligochaeta n. sp.
Figure 28

Material examined
Rennison Island, British Columbia (52°51'N, 129°21'W), Bousfield 1964 stn. H30, 20 July 1964. 7.2–21.6 m dredge over sand and kelp. Holotype, ♂, NMC-C-1981-936: allotype, ♂, NMC-C-1981-937, paratypes, 23 ♂♂, 21 ♀♀, NMC-C-1981-938.

Additional material
Alaska — southeastern coast: 4 ♂♂, 4 ♀♀, 1 immature from Bousfield 1980 stn. S23F1.

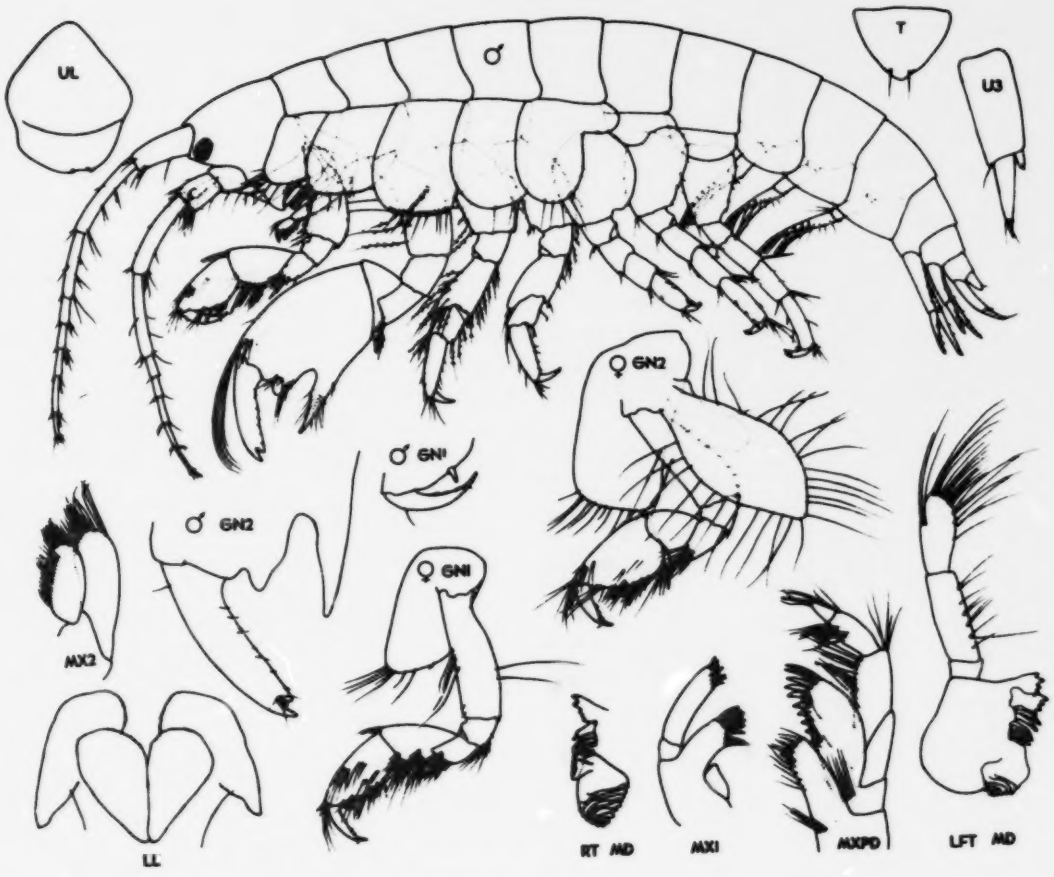


Figure 28. *Photis oligochaeta* n. sp. ♂ 3.3 mm, ♀ 3.5 mm, Rennison Is., B.C.

British Columbia — northern mainland: 55 ♂♂, 42 ♀♀, 2 immatures from Bousfield 1964 stns. H5, H8 (2 ♂♂, 3 ♀♀ deposited in the Zoological Institute, Leningrad), H22, H26, H30, H65 (3 ♂♂, 5 ♀♀ deposited in the Smithsonian Institution (USNM)); Vancouver Island: 1 ♂ from Bousfield 1970 stn. P721.

Diagnosis

Holotype, male, 3.3 mm: Eye medium; antennae 1 and 2 moderately setose, antenna 2 peduncular segment 4 not anteriorly inflated: coxae, lower margins moderately setose; coxae 1 and 2 shallower than coxae 3–5, coxa 2 intermediate in depth between 1 and 3; lower margins of coxae 1 and 2 straight, parallel with the body mid-line; gnathopod 1, segment 5 about equal to segment 6, posterior margin broad, more than half the length of the anterior margin; segment 6, palm oblique; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a single long defining tooth which extends beyond the palm; palmar excavation broadly conical, hinge tooth cylindrical; dactyl overlapping the palm somewhat, inner margin strongly notched distally, but otherwise fairly straight and lacking a medial protuberance; coxa 3, lower margin bearing stridulation ridges.
Size range — male to 3.3 mm.
Diagnosis of the female allotype, 3.5 mm: Gnathopod 1, segment 5 about equal in length to segment 6, the posterior lobe about half the length of the anterior margin; segment 6 narrow, palm convex; gnathopod 2, palm convex; segment 2 and coxa 3 lacking stridulation ridges; other features similar to the male.
Size range — female 2.5 to 3.5 mm.

Distribution

Taigud Island, Alaska (56°54.5′N, 135°24′W) south to East Sooke, Vancouver Island, B.C. (48°22′N, 123°43′W).

Ecology
A cold water species found on protected coasts over sand and gravel at low water level to 21.6 m depth. Temperatures recorded in the collections of Bousfield, 1964–1980, were 9.8–12.0°C, salinities 31.5–32.1°/oo.

Life history
Females ovigerous in July and August.

Etymology
Gr: *oligo* = few, *chaeta* = hairs, referring to the paucity of setae on the lower margins of the coxae. This feature may be size related as generally the larger species are also more setose.

Photis pachydactyla n. sp.
Figure 29

Material examined
Broken Islands, west side of Wouwer Is., Barkley Sound, Vancouver Is., B.C. (48°51.6'N, 125°21.8'W). Bousfield 1976 stn. B7. Bedrock, *Phyllospadix*, kelp, etc. Under rocks, *Phyllospadix* holdfast, boulders. 12°C, 32+ °/oo. Holotype, ♂, NMC-C-1981-939; allotype, ♀, NMC-C-1981-940; paratypes, 7 ♂♂, 9 ♀♀, 5 immatures, NMC-C-1981-941.

Additional materia
Alaska — southeastern coast: 1 ♂, 1 ♀ from Bousfield 1961 stns. A171–2.
British Columbia — Queen Charlotte Islands: 1 ♂, 4 ♀♀, 1 immature from Bousfield 1957 stn. W12; northern mainland: 8 ♂♂, 10 ♀♀ from Bousfield 1964 stn. H1; southern mainland and Vancouver Island: 9 ♂♂, 10 ♀♀, 5 immatures from Bousfield 1976 stns. B7, B28; 1 ♂, 1 ♀, 3

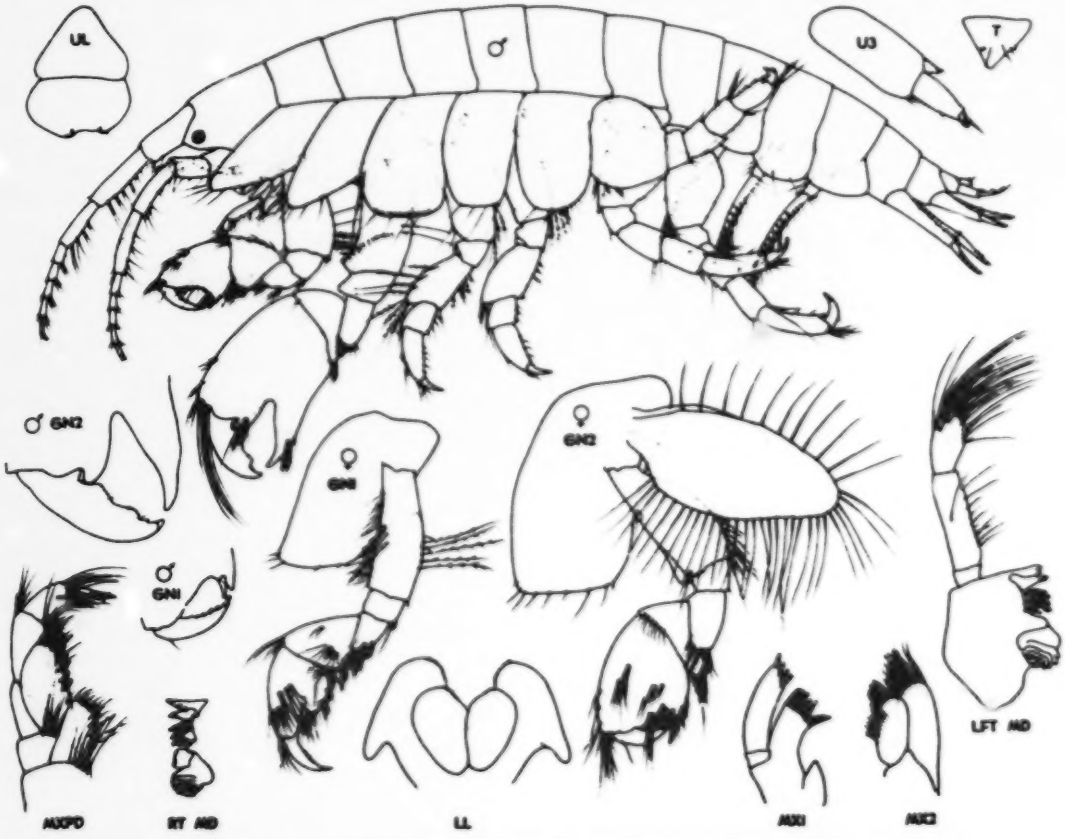


Figure 29. *Photis pachydactyla* n. sp. ♂ 4.0 mm, ♀ 4.0 mm, Broken Islands, Barkley Sound, Vancouver Is., B.C.

immatures from Bousfield 1975 stn. P16b; 1 ♂, 4 ♀♀, 1 immature from Bousfield 1957 stn. W12 (deposited in the Zoological Institute, Leningrad), 2 ♂♂, 2 ♀♀ from the collection of W.C. Austin (NMC acc. no. 1976–158, deposited in the Smithsonian Institution (USNM)); 1 ♂ from the collection of C.D. Levings.

Diagnosis

Holotype, male, 4.0 mm: Eye small; antennae 1 and 2 moderately setose, antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins moderately setose; coxae 1 and 2 as deep as coxae 3–5, lower margins angled 45° to the body mid-line; gnathopod 1, segment 5 shorter than segment 6, posterior margin about half the length of the anterior margin; segment 6, palm deeply concave; gnathopod 2, segment 2 anterodistally produced to a pointed lobe bearing stridulation ridges; segment 6 with a single long defining tooth which extends beyond the palm; palmar excavation broadly conical, hinge tooth cylindrical; dactyl heavy, not overlapping the palm, inner margin sinuous, cusped and finely notched; coxa 3, lower margin bearing stridulation ridges.

Size range: up to 4.0 mm.

Allotype, female, 4.0 mm: gnathopod 1, segment 5 subequal to segment 6, posterior lobe about half the length of the anterior margin; segment 6, palm convex; gnathopod 2, palm excavate, sinuous; segment 2 and coxa 3 lacking stridulation ridges. Other features similar to the male.

Size range: 3.0 to 4.0 mm.

Distribution

Puffin Bay, Alaska (56°16′N, 134°48′W) south to Edward King Island, Barkley Sound, Vancouver Island, B.C. (48°49.08′N, 125°12.05′W).

Ecology

Occurs on exposed and semi-protected coasts on rocky substrates at low water level to 90 m depth. Temperatures recorded in the collections of Bousfield, 1961–1976, were 10.5–12°C, salinities 23–32 °/oo.

Life history

Females ovigerous in July and August.

Remarks

The male is clearly distinguishable, even when immature, by the strongly concave palm of the first gnathopod which posteriorly hooks downward to meet the dactyl.

Etymology

Gr.: *pachy* = thick, *dactyl* = finger; referring to the heavier than usual dactyl of the male second gnathopod.

Photis parvidons n. sp.
Figure 30

Material examined

Off Cape Beale, mouth of Trevor Channel, Barkley Sound, Vancouver Island, B.C. Bousfield 1977 stn. B17, 30 May 1977. 36–40 m depth. Holotype, ♂, NMC-C-1981-930; allotype, ♀, NMC-C-1981-931; paratypes, 26 ♂♂, 32 ♀♀, 22 immatures, NMC-C-1981-932.

Additional material

British Columbia — northern mainland: 7 ♂♂, 14 ♀♀, 16 immatures from Bousfield 1964 stn. H12; southern mainland and Vancouver Island: 47 ♂♂, 51 ♀♀, 47 immatures from Bousfield 1977 stns. B17, B18, B19a, B19b, E5, P3; 23 ♂♂, 33 ♀♀, 60 immatures from Bousfield 1976 stns. B16, B20, B28; 96 ♂♂, 90 ♀♀, 50 immatures from Bousfield 1975 stns. P8 (13♂♂, 8 ♀♀, 4 immatures deposited with the Smithsonian Institution (USNM)), P10 (3 ♂♂, 4 ♀♀, 1 immature deposited in the Zoological Institute, Leningrad), P21a, P21b, P22.

Washington: 2 ♂♂, 5 ♀♀ from Bousfield 1966 stn. W40.

Diagnosis

Male holotype, 4.5 mm: Eye medium; antennae 1 and 2 moderately setose, antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins strongly setose; coxae 1 and 2 shallower than coxae 3–5, lower margins straight, parallel with the body mid-line; gnathopod 1, segment 5 subequal to segment 6, posterior lobe half the length of the anterior margin, segment 6 rather narrow, palm concave; gnathopod 2, segment 2 bearing stridulation ridges; segment 6 with a single defining tooth which reaches to the theoretical depth of the palm as defined by the anterodistal margin of the segment; palmar excavation narrow, hinge tooth pointed; dactyl hardly overlapping the palm, inner margin bearing a cusp at the junction of the unguis and a small protuberance centrally; coxa 3, lower margin bearing stridulation ridges.

Size range: male to 5.0 mm.

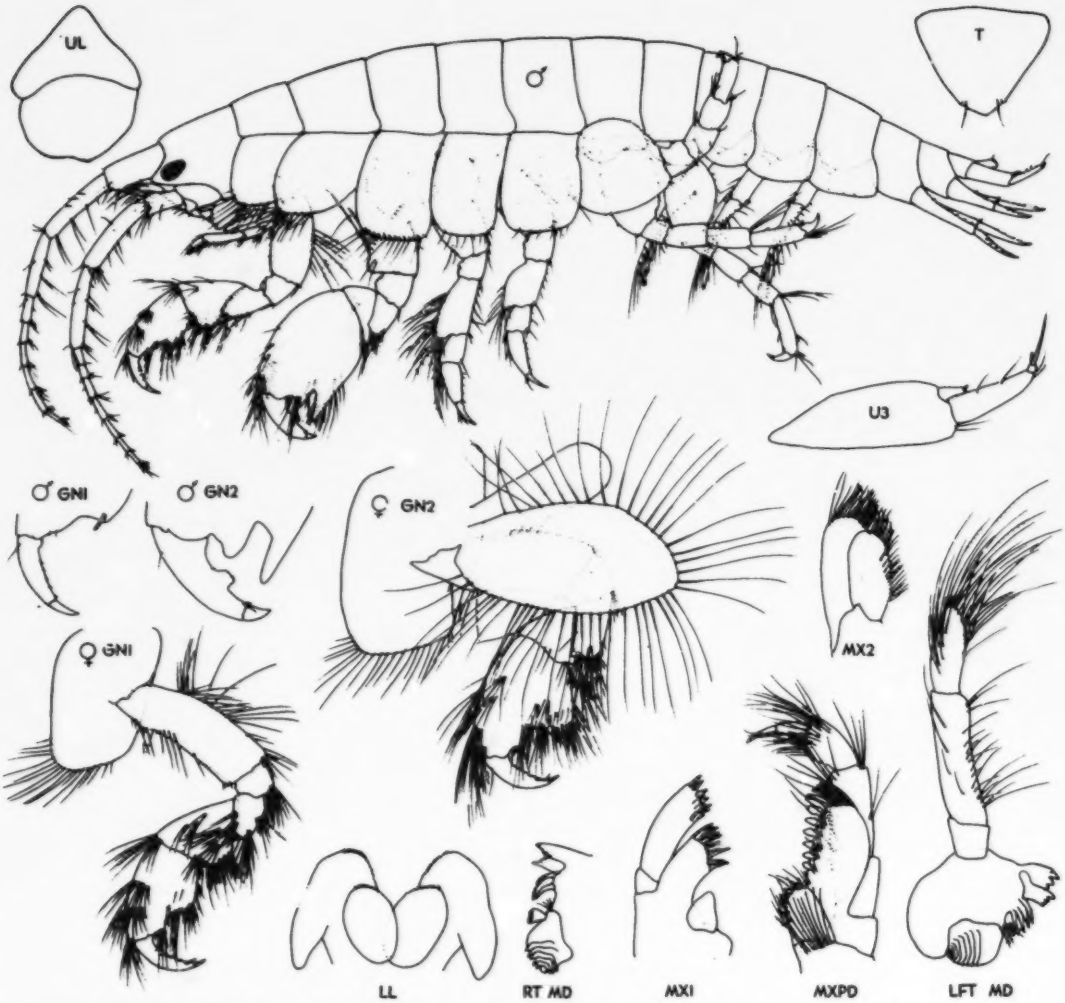


Figure 30. *Photis parvidons* n. sp. ♂ 4.3 mm, ♀ 4.0 mm, Cape Beale, Barkley Sound, Vancouver Is., B.C.

Allotype, female, 6.0 mm: Gnathopod 1, segment 5 somewhat shorter than segment 6, posterior lobe about half the length of the anterior margin; segment 6, palm concave; gnathopod 2, palm concave, segment 2 and coxa 3 lacking stridulation ridges, other features similar to the male.
Size range: female 3.5 to 6.0 mm.

Distribution
Northern British Columbia (Stephens Is. (54°11′N, 130°48′W) south to Mukkaw Bay, Washington (48°19′N, 124°40′W).

Ecology
Occurs on exposed and semi-protected coasts mainly on sandy sediments at low water level to 54 m depth. Temperatures recorded by Bousfield, 1964–1977, were 8–12.3°C, salinities 30.4–33 °/oo.

Life history
Females ovigerous from May to November.

Remarks
This species is similar to *Photis brevipes* but differs in the following respects: in the male, gnathopod 1 is slenderer and segment 5 is more narrowly lobed; gnathopod 2 is also slenderer, the palmar incision is narrower and the hinge tooth is pointed, rather than square; the dactyl tooth is also smaller; in the female, the palm of gnathopod 1 is concave, rather than oblique and in

gnathopod 2 is more strongly excavate. The males of this species can be differentiated from immature *P. brevipes* only on the basis of size. In younger females of this species the palms of gnathopods 1 and 2 are less excavate and thus are indistinguishable from females of *P. brevipes*. Evidently, these species are close relatives.

Etymology

L.: *parvi* = small, *dons* = tooth; referring to the small medial tooth on the dactyl of the male gnathopod 2.

***Photis* cf. *spasskii* Gurjanova**
Figure 31

Photis spasskii Gurjanova, 1951, pp. 848–849, fig. 594.

Material examined

Alaska — Bering Sea: 1 ♂, 1 ♀ from P. Slattery collection northeast of St. Lawrence Is., 10 July 1980; southeastern coast: 218 ♂♂, 152 ♀♀, 13 immatures from Bousfield 1961 stns. A8, A30, A32, A33 (representative specimens deposited in the Smithsonian Institution and Leningrad Museum), A83.

British Columbia — Queen Charlotte Islands: 2 ♂♂, 9 ♀♀, 13 immatures from Bousfield 1957 stn. H3; northern mainland: 1 ♂, 2 ♀♀, 1 immature from Bousfield 1964 stn. H13.

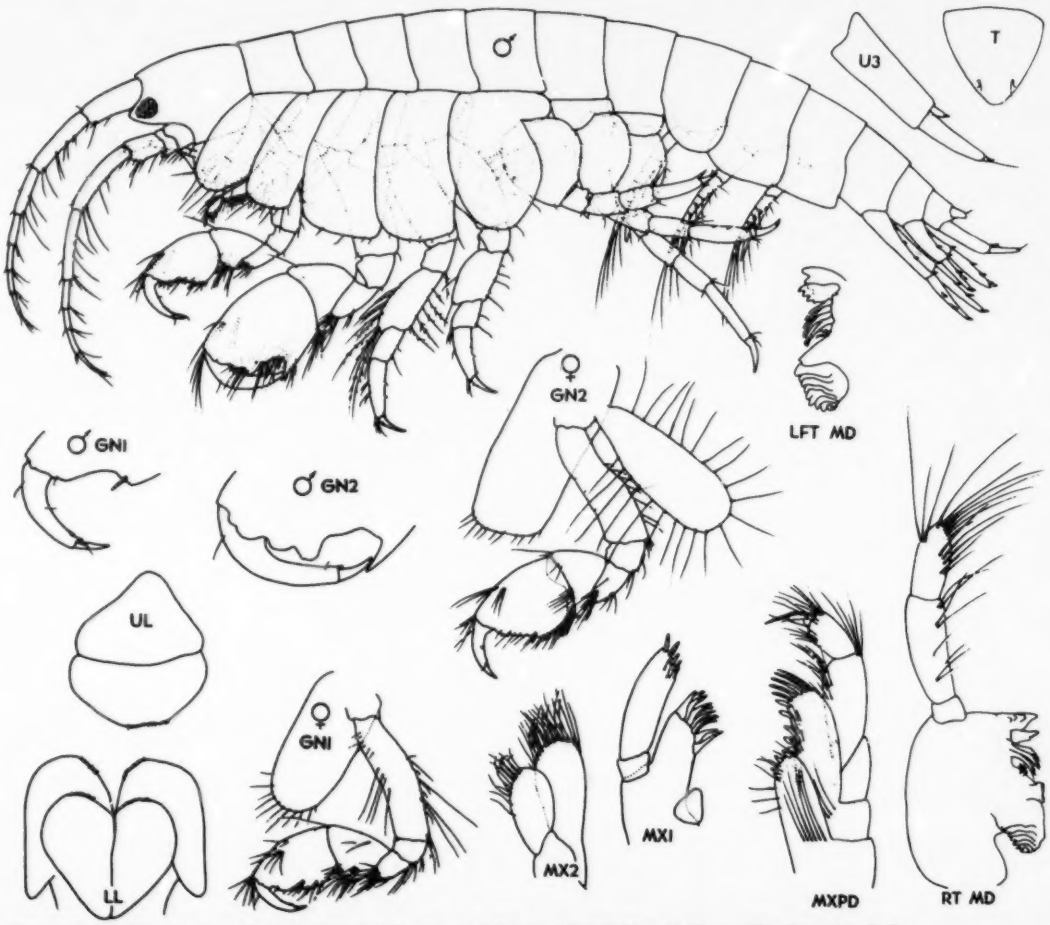


Figure 31. *Photis* cf. *spasskii* Gurjanova ♂ 3.0 mm, ♀ 3.0 mm, Masset Sound, Queen Charlotte Is., B.C.

Diagnosis

Male: eye medium; antennae 1 and 2 moderately setose; antenna 2 peduncular segment 4 not anteriorly inflated; coxae, lower margins weakly setose; coxae 1 and 2 hardly shallower than coxae 3–5, with coxa 2 intermediate in depth between coxae 1 and 3; lower margin of coxa 1 rounded, coxa 2 straight; gnathopod 1, segment 5 shorter than segment 6, posterior lobe narrow, less than half the length of the anterior margin; segment 6 fairly broad, palm concave; gnathopod 2, segment 2 lacking stridulation ridges; segment 6 with a single narrow defining tooth which reaches the depth of the palm; palmar excavation rounded; two palmar hinge teeth, each shallow and square; dactyl evenly convex and not overlapping the palm; inner margin of the dactyl bearing a cusp at the junction of the unguis, but lacking a protuberance. Coxa 3, lower margin lacking stridulation ridges.

Female: gnathopod 1, segment 5 shorter than segment 6, posterior lobe narrow, less than half the length of the anterior margin; segment 6, palm convex; gnathopod 2, palm convex; other features similar to the male.

Size range: male to 4.5 mm, female 3.0 to 4.0 mm.

Distribution

Northeast of St. Lawrence Island, Bering Sea (64°N, 169°W) south to Lelu Island, B.C. (54°12′N, 130°18′W). Also recorded in the U.S.S.R. off the east coast of Kamchatka (55°N, 163°E).

Ecology

An Arctic species occurring on exposed and semi-protected coasts at low water level to 21 m depth. Temperatures recorded by Bousfield, 1957 and 1961, were 6.3 to 12.0°C, salinities 14.3 to 29.9 °/oo.

Life history

Females ovigerous from June to August.

Remarks

The specimens studied herein differ in the following respects from the type description of Gurjanova (1951): gnathopod 1 of the female bears a small obturator spine and the dactyl is lightly cusped; gnathopod 2 of the female is convex rather than concave as in Gurjanova's specimens; in the male, segment 5 of gnathopod 1 is not as narrowly lobed and the palm is concave, rather than convex; peraeopod 6 is shorter than 7 and in both peraeopods segment 6 is longer than segment 5, rather than equivalent. The form of the second gnathopod is similar in both east and west Pacific males, and since the characteristics of this appendage are so heavily relied upon in species diagnosis for this genus, the author hesitates to elevate the North American material to specific status. In addition, there may be some question of confusion in the labelling of gnathopods in Gurjanova's fig. 594. Reversal of labelling of the female gnathopod 2 with the male gnathopod 1 would make these appendages virtually identical to the material at hand.

Genus ***Chevalia*** Walker

Chevalia Walker, 1904, pp. 288–290, pl. 7, fig. 50, pl. 8, fig. 50; J.L. Barnard, 1973, p. 16.
Neophotis Stout, 1913, p. 653.

Type species

Chevalia aviculae Walker, 1904.

Additional species

This is the only species known for this genus. *Chevalia mexicana* Pearse and *Neophotis inaequalis* Stout were synonymized with *C. aviculae* by J.L. Barnard (1962).

Diagnosis

Body strongly laterally compressed, vermiform. Body plates 1–3 acutely produced posterodistally. Peraeon 6–7 and pleon segments greatly enlarged. Head lobe rounded, antennal sinus shallow. Eye medium, elliptical. Antenna 1 peduncular segment 3 nearly as long as segment 1; accessory flagellum reduced; flagellum 2 somewhat shorter than flagellum 1. Upper lip, epistome produced but not acutely. Mandibular palp segment 3 slender, not clavate; molar with 4 raker spines. Maxilla 1, inner plate setose. Maxilla 2 bearing facial setae. Coxae not contiguous, smaller than the body plates, shallowing posteriorly, not setose. Coxa 1 produced forward; coxa 3 lacking stridulation ridges. Gnathopod 1, segment 5 longer than segment 6, not posteriorly lobed; palm indistinct, dactyl much longer than the palm. Gnathopod 2, segment 2 lacking stridulation ridges; segment 5 shorter than segment 6 and produced into a narrow posterior lobe; segment 6 not sexually dimorphic. Peraeopods 3 and 4, segment 4 inflated,

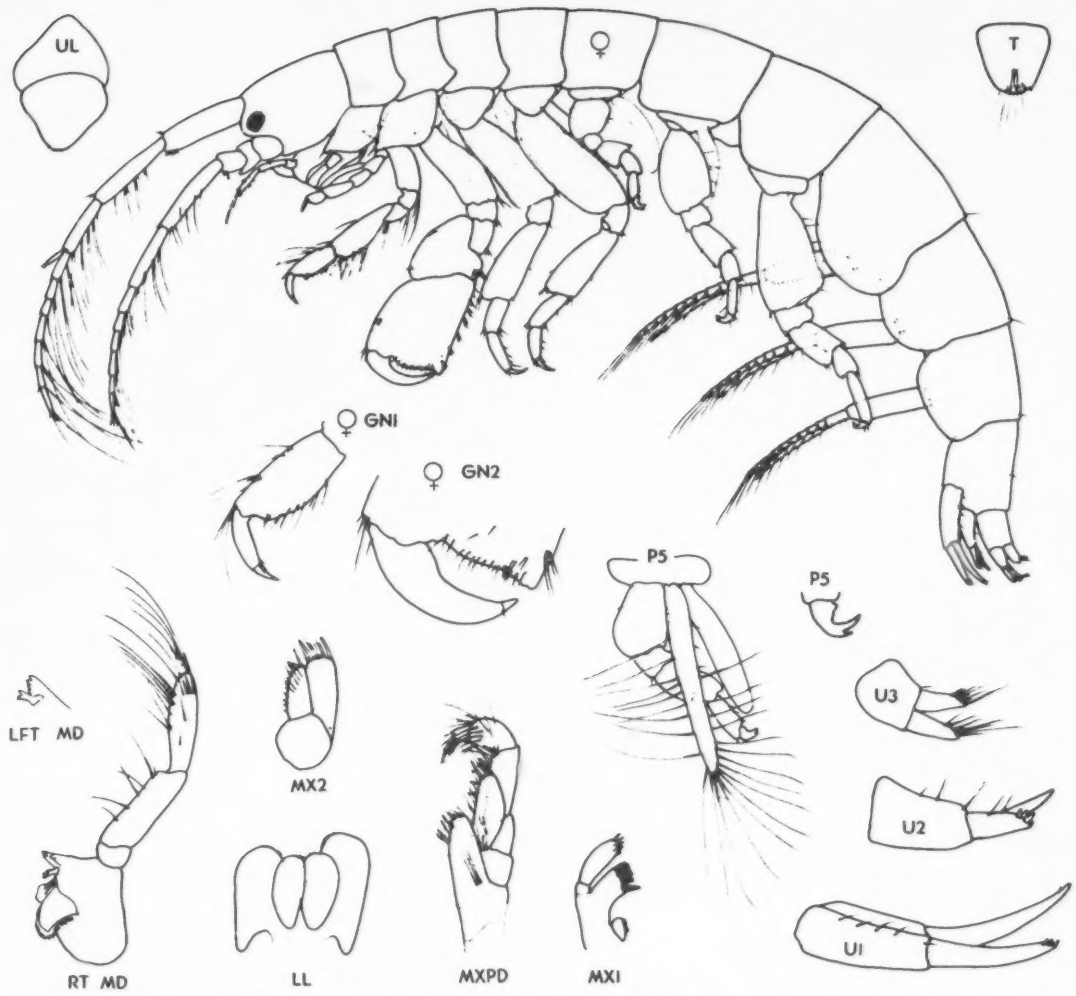


Figure 32. *Chevalia aviculae* Walker ♀ 3.8 mm, Bauke Is., Barkley Sound, Vancouver, Is., B.C.

twice as long as, but not overhanging segment 5. Peraeopods 5–7 very small; dactyl bearing an accessory tooth. Peraeopod 5, segment 2 not posterodistally notched. Peraeopods 6 and 7 progressively larger than peraeopod 5; segment 2, hind margin not setose; segment 5 lacking comb spines. Pleopods normal. Epimera not posterodistally notched, lacking a lateral ridge; pleon segments each bearing a pair of setae dorsally. Urosome dorsally smooth, segments 1 and 2 fused. Uropod 1 peduncle bearing a posteroventral spinous process; uropods 1 and 2, inner rami not terminally spinose. Uropod 3 short; rami extending equally. Telson bearing a pair of small apical cusps and a number of setae. Brood plates narrow, linear; setae not hook-tipped. Small size (3.8 to 5.0 mm).

Distribution

Circumtropical, having been collected in the Indian Ocean, South Africa, Caribbean Sea and eastern Pacific Ocean. This new record from Barkley Sound, B.C. sets the northernmost limit of the genus.

Chevalia aviculae Walker
Figure 32

Chevalia aviculae Walker, 1904, pp. 288–290, pl. 7, fig. 50, pl. 8, fig. 50; Walker, 1909, p. 341; K.H. Barnard, 1916, p. 252; Shoemaker, 1921, p. 101; K.H. Barnard, 1937, p. 169, fig. 15; Shoemaker, 1941, p. 87; 1942, p. 39; J.L. Barnard, 1962, pp. 17–20, fig. 5; 1964, p. 236.

Chevalia mexicana Pearse, 1912, pp. 374–376, fig. 5
Neophotis inaequalis Stout, 1913, pp. 653–654.

Material examined
British Columbia — Vancouver Island; 1 ♀ in B.C. Provincial Museum collection, BCPM 973-166-34N, southeastern corner of Bauke Island, Barkley Sound (48.5°N, 125.0°W), 10 July 1973. Scuba collection at 10 m depth or less, over rocky, shelly bottom; algae, high salinity, semi-exposed.

Diagnosis
Female: accessory flagellum 2-segmented; coxae small, discontiguous, coxa 5 smaller than coxa 4; gnathopod 2, segment 5 anterodistally bulging; segment 6, palm bearing a low protuberance and defining tooth; dactyl shorter than the palm; peraeopods 5–7, segments 2 and 4 inflated.
Size range: 3.8 to 5.0 mm (both sexes).

Distribution
Circumtropical — Indian Ocean, South Africa, Caribbean Sea, eastern Pacific Ocean (48.5°N, 125.0°W south to 32.5°N, 117.5°W).

Ecology
A tropical to warm temperature species occurring amongst algae and amongst kelp holdfasts, rarely deeper than 10 m depth.

Remarks
The collection locality of this specimen marks the northernmost limit of distribution of this species. Barnard (1973) states that the species has no close relative.

Discussion and Conclusions

Biogeography

Table 1 summarizes the geographic distribution of the Isaeidae occurring in the northeastern Pacific from Alaska to Pt. Conception, California. Greatest diversity is in central and southern British Columbia (61% of the total). One is tempted to correlate these high numbers with greater intensity of sampling in B.C. However, despite the very limited collections from Alaska, nearly as many species (58%) were identified. Calculation of the percentage of species in common with each neighbouring district shows that the Isaeidae of the Bering Sea are distinctive, comprising 6 circum-Arctic and pan-Pacific species and 6 endemic species. By comparison, from southern Alaska to Washington, the family comprises mainly endemic and southern species reaching their northerly limits here. Oregon and northern California Isaeidae are apparently more regionalized but this may be due to insufficient sampling as most species present occur in disjunct groups farther north.

Amongst the genera, it is evident from Table 1 that *Gammaropsis* is a southern genus penetrating north only to southern Alaska. *Paraeurystheus, Podoceropsis, Photis, Protomedeia* and *Cheirimedeia* are broadly ranging northern genera. None is endemic to the American coast and only *Paraeurystheus* and *Cheirimedeia* are restricted to the Pacific. *Chevalia* is more commonly a tropical genus and this new record in British Columbia extends its eastern Pacific range far north. The ranges of the regional species can be summarized as follows:

1. Pan-Arctic, comprising three species of *Protomedeia*: *P. fasciata, P. grandimana* and *P. stephenseni*.
2. Pan-Pacific, further subdivisible into
   a) sub-Arctic species *Paraeurystheus tzvetkovae, Paraeurystheus dentatus, Photis fischmanni* and *Photis* cf. *spasskii*
   b) boreal species *Podoceropsis barnardi* and *Cheirimedeia macrocarpa americana*
3. American-endemic, further subdivisible into
   a) sub-Arctic species *Paraeurystheus tzvetkovae, Paraeurystheus dentatus, Podoceropsis amchitkensis, Podoceropsis setosa, Podoceropsis chionoecetophila, Cheirimedeia macrodactyla* and *Cheirimedeia similicarpa*
   b) northern boreal, species, comprising the majority of the regional species, *Gammaropsis shoemakeri, Gammaropsis ellisi, Gammaropsis spinosa, Gammaropsis thompsoni, Podoceropsis angustimana, Photis bifurcata, Photis brevipes, Photis lacia, Photis macinerneyi, Photis oligochaeta, Photis pachydactyla, Photis parvidons, Cheirimedeia zotea* and *Protomedeia prudens*
   c) southern boreal species, *Photis conchicola* and *Protomedeia articulata*.
   d) the mainly tropical species *Chevalia aviculae*.

Distributional Ecology and Notes on Behaviour

Table 2 indicates that the regional Isaeidae are relatively narrowly stenotopic, ranging bathymetrically from the low intertidal to considerable subtidal depths, but otherwise generally limited to surf-exposed situations in moderate to high salinities. Since the Isaeidae are not restricted to the photic zone, substrata for tube construction must be varied. In *Podoceropsis*, at least, the commensal habit has developed. Southern species trend to greater eurytopicity and occur more frequently in wave-protected and lower salinity habitats. Southern species of *Gammaropsis* also trend towards a shallower depth range.

Very little is known of the living and feeding behaviour of isaeids. Although the group members are primarily tube-dwellers, the elongated glandular dactyls of *Protomedeia* and *Cheirimedeia* indicate a specialized tube construction function. None of the regional Isaeidae possesses the broadly expanded glandular segment 2 of peraeopods 3 and 4 that occurs in the more advanced tube spinners Ampithoidae and Corophiidae. Several morphological characters seem functional in reducing the exposure of the body from the tube. The hook-like third uropod of *Photis*, the toothed peraeopod 5–7 dactyls of *Chevalia* and *Photis* and the dorsal cuspation in *Paraeurystheus* and *Gammaropsis* would serve in grasping the tube and allowing quick withdrawals into it. The shallowing of the coxae and flattening of *Protomedeia, Cheirimedeia* and *Chevalia* well adapt the body to a cylindrical tube. The possession of stridulation ridges by *Photis* would serve in communica-

tion and sexual attraction. The long and densely setose antennae of *Gammaropsis, Podoceropsis* and *Photis* would extend the range for collection of sensory information while the lengthened ocular lobes would increase the ability to see from the tube aperture by a slight margin. The opposite strategy, highly developed in the Corophiidae, is visible in *Protomedeia* and *Cheirimedeia* where the second antennae shorten and thicken for food gathering. Barnard (1973) and Myers (1980) see the differing head and antennal developments of the *Gammaropsis* and *Protomedeia* groups as being of basic significance to the dichotomous evolution of the Corophioidea.

Taxonomic Considerations

The phyletic positions of regional genera of the Isaeidae are examined in Table 3 and Fig. 33 based on the plesio-apomorphic states of characters judged to be of generic significance. Many of the character diagnoses were based on the analyses of Barnard (1973), Bousfield (1977, 1979b) and Myers (1981). Thus the ancestral, or plesiomorphic amphipod would bear an unmodified head without extended ocular lobes, shallow antennal sinus, two pairs of similar, slender antennae, short peduncular segment 3 on antenna 1, multisegmented accessory flagellum, smooth, unflattened body with large coxae, large, reniform eye, basic mouthparts with fully developed, fully setose and spinose plates and palps, gnathopods strongly subchelate with an elongate, shallow carpal lobe, simple peraeopods possessing a peduncular spinous process on uropod 1, and equally sized setose and spinose rami of uropod 3. Other features, such as the structure of peraeopods 3 and 4 and the brood plates were derived by comparison with more apomorphic corophioidean descendants and more plesiomorphic gammaroidean precursors. For instance, the shortened fifth segment of peraeopods 3 and 4 occurs in the more apomorphic Ischyroceridae and Corophiidae and also in the apomorphic Ampeliscoidea and Phoxocephaloidea but not in the primitive ancestral Dexaminoidea and Gammaroidea and therefore can be termed apomorphic. Similarly, hooking of the brood setae occurs in the more apomorphic Ampithoidae but not in the more plesiomorphic Gammaroidea. However a broad knowledge of a character range is necessary to avoid the pitfalls of convergence. Some characters, as well, may be phyletically consistent in the majority but suddenly reverse to the assumed primitive form in otherwise highly apomorphic species (viz. brood plate variability, Bousfield (1979b, 1982b). Because the fossil record of the Amphipoda is scant, there is a speculative element in the determination of absolute apomorphy and it was therefore felt inadvisable to attempt a character-state analysis below the generic level. The values presented in Table 3 are therefore subject to alteration through addition of new characters, differential weighting of the characters, altered character-state assumptions and additional taxa from elsewhere. Large differences in value, as occur between *Paraeurystheus — Gammaropsis* and *Podoceropsis — Protomedeia — Cheirimedeia — Chevalia — Photis* are probably significant.

Cluster analysis, utilizing the characters in Table 3, produces a graphic indication of phenetic and semi-phylogenetic relationships of regional genera of the Isaeidae in Fig. 33 *Paraeurystheus* and *Gammaropsis* are the most primitive of the regional genera and are the basis for differentia-

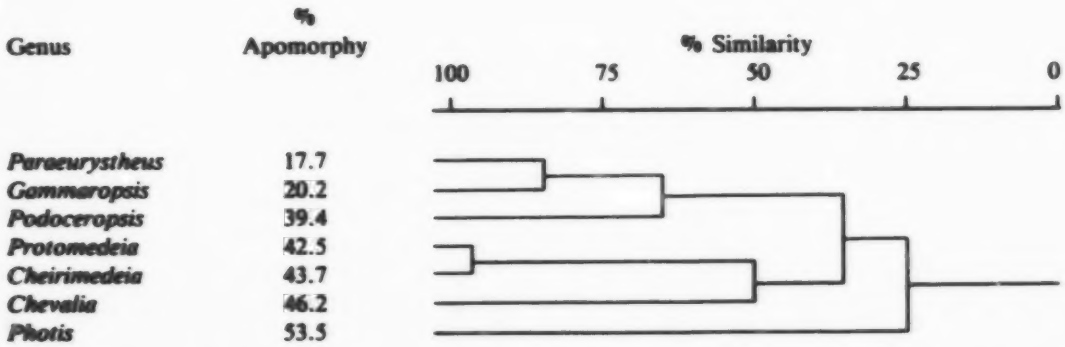
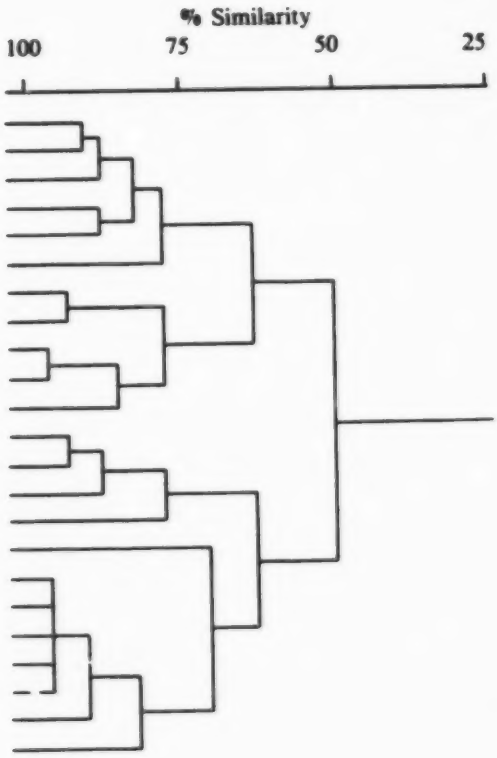


Figure 33. Phenogram produced by cluster analysis of regional Isaeidae. Percentage apomorphy was computed from 47 generic level characters described in Table 3.

tion of the considerably more apomorphic *Podoceropsis*. *Protomedeia* and the close relative *Cheirimedeia* lie distinct from the *Gammaropsis* group. *Chevalia* links at a 50% similarity level to the *Protomedeia-Cheirimedeia* group. Although computed to be hardly more apomorphic, weighting of such unique characters as the fused urosomites, vermiform body shape, small, discontiguous coxae and reduced hind peraeopods would better illustrate the distinctiveness of *Chevalia*. *Photis* is the most apomorphic of the regional genera and links last to the group as a whole. Barnard (1973) postulates, on the basis of head structure, that *Photis* was derived from the *Gammaropsis* line.

The results of cluster analysis of the regional, type and some neighbouring species for the *Gammaropsis* group, *Protomedeia* group and *Photis* are illustrated in Figs. 34, 35 and 36, respectively. The figures are not comparable because only species-specific characters appropriate to each group were selected. This selectivity optimizes the differences between species but the significance of these differences must be subjectively evaluated.

Geographic Distribution	Species
1	*Paraeurystheus gurjanovae*
1	*Paraeurystheus anamae* (Type species)
1, 2	*Paraeurystheus dentatus*
1	*Paraeurystheus sexdentatus*
2	*Paraeurystheus tzvetkovae*
1	*Paraeurystheus latipes*
1	*Gammaropsis gurvitzi*
3, 4	*Gammaropsis ellisi*
6	*Gammaropsis tonichi*
3, 4, 5, 6	*Gammaropsis thompsoni*
4, 5	*Gammaropsis shoemakeri*
2, 7	*Gammaropsis melanops*
7	*Gammaropsis maculata* (Type species)
6	*Gammaropsis mamola*
4, 5, 6	*Gammaropsis spinosa*
6	*Gammaropsis ventosa*
4	*Podoceropsis angustimana*
4	*Podoceropsis barnardi*
2	*Podoceropsis amchitkensis*
2	*Podoceropsis setosa*
7	*Podoceropsis lindahlii*
2, 5	*Podoceropsis chionoecetophila*
7	*Podoceropsis sophiae* (Type species)



Key:
1. U.S.S.R., Japan
2. Bering Sea
3. Southern Alaska
4. British Columbia
5. Washington, Oregon and Northern California
6. Southern California
7. Atlantic

Figure 34. Phenogram produced by cluster analysis of regional species of *Paraeurystheus*, *Gammaropsis* and *Podoceropsis* using 37 species and generic level characters. Neighbouring species from the U.S.S.R. and southern California, and Atlantic type species are added for comparison.

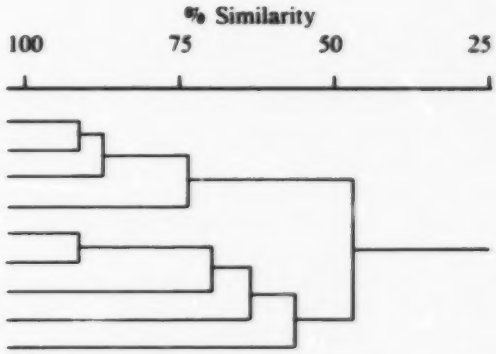
Fig. 34 illustrates that the shifting of *Paraeurystheus gurvitzi* to the genus *Gammaropsis* and of *Gammaropsis dentata* to *Paraeurystheus* is justified. This move had been suggested, but not executed, by Tzvetkova (1977), in formulating the genus *Paraeurystheus*. Within the genus *Gammaropsis*, two groups are evident which bear geographic distinction as well. The more plesiomorphic group (Table 3) bears closer resemblance to *Paraeurystheus* and occurs in northern waters of B.C. and Alaska while the more apomorphic group bears closer resemblance to *Podoceropsis* and ranges from lower B.C. south to Baja California. Morphologically, the northern group is distinguished by a larger, reniform eye, non-reduced segment 5 of peraeopods 3 and 4, and cusping of the epimera and urosome, features which occur also in *Paraeurystheus*. Taxonomic subdivision of *Gammaropsis* is therefore warranted. Barnard (1973) added considerable confusion to the taxonomy of the genus by including *Audulla, Bonnierella, Kermystheus, Megamphopus, Podoceropsis* and *Pseudeurystheus* as subgenera, by reason that no single character consistently distinguished the groups. Figs. 33 and 34 show that at least between *Paraeurystheus* and *Podoceropsis*, regional distinctions are clearly definable.

The phenogram produced by cluster analysis of regional species of *Protomedeia* and *Cheirimedeia* is shown in Fig. 35. The generic subdivision is clear but not further subgrouping seems incipient. As could be expected, the more plesiomorphic and broadly distributed *Protomedeia* is also morphologically more diverse.

Cluster analysis of regional species of *Photis* (Fig. 36) distinguishes four groups which break on the basis of morphology of the gnathopods. Since these characters are highly variable and in part sexually-related, they probably are of lesser significance in justifying taxonomic recognition of the groups.

Barnard (1973) and Myers (1981) speculate that *Gammaropsis* and *Protomedeia* are the basic stocks for dichotomous evolution in the Corophioidea, with *Gammaropsis* leading to the bulk of the Isaeidae, Neomegamphopidae, Ampithoidae and Ischyroceridae, and *Protomedeia* leading to the Aoridae and Corophiidae. *Gammaropsis* is a predominantly tropical genus while *Protomedeia* is predominantly boreal (Barnard, 1973). Regionally, *Paraeurystheus* was probably

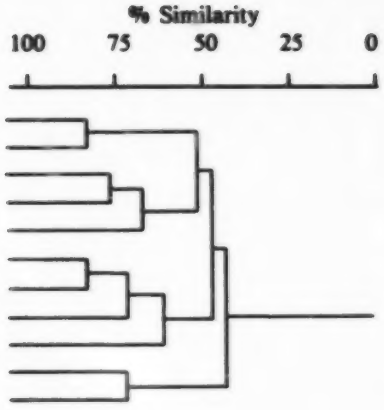
Geographic Distribution	Species
5, 6	*Cheirimedeia zotea* (Type species)
2, 4	*Cheirimedeia similicarpa*
4, 5	*Cheirimedeia macrocarpa americana*
2	*Cheirimedeia macrodactyla*
2, 7	*Protomedeia stephenseni*
1, 3, 4, 7	*Protomedeia grandimana*
5, 6	*Protomedeia articulata*
2, 7	*Protomedeia fasciata* (Type species)
4, 5, 6	*Protomedeia prudens*



Key:
1. U.S.S.R., Japan
2. Bering Sea
3. Southern Alaska
4. British Columbia
5. Washington, Oregon and Northern California
6. Southern California
7. Atlantic

Figure 35. Phenogram produced by cluster analysis of regional species of *Protomedeia* and *Cheirimedeia* using 30 species and generic level characters.

Geographic Distribution	Species
4, 5	*Photis macinerneyi*
1, 2, 3	*Photis* cf. *spasskii*
1, 2	*Photis fischmanni*
4, 5	*Photis parvidons*
7	*Photis reinhardi* (Type species)
3, 4	*Photis oligochaeta*
4, 5, 6	*Photis lacia*
5, 6	*Photis conchicola*
3, 4, 5, 6	*Photis brevipes*
3, 4, 5, 6	*Photis bifurcata*
3, 4	*Photis pachydactyla*



Key:
1. U.S.S.R., Japan
2. Bering Sea
3. Southern Alaska
4. British Columbia
5. Washington, Oregon and Northern California
6. Southern California
7. Atlantic

Figure 36. Phenogram produced by cluster analysis of regional species of *Photis* using 24 species level characters. The Atlantic type species is added for comparison.

an early derivative of a proto-*Gammaropsis*, while *Podoceropsis* and *Photis* were derived separately. Barnard (1973) places *Chevalia* on the *Protomedeia* line but notes that there are no close relatives. Myers (1981), however, links this genus to the *Gammaropsis* line. Fig. 33 supports Barnard's (1973) hypothesis. The broad northern range of *Protomedeia* suggests an Arctic dispersal with subsequent derivation of *Cheirimedeia* in the North Pacific.

References

Alderman, A.L. 1936. Some new and little known amphipods of California. University of California Publications in Zoology, 41(4): 53–74.

Barnard, K.H. 1916. Contributions to the crustacean fauna of South Africa, 5: The Amphipoda. Annals of the South African Museum, 15: 105–302.

_____ **1937.** Amphipoda. *In*: Scientific Reports. The John Murray Expedition, 1933–34, 4(6): 131–201.

Barnard, J.L. 1954. Marine Amphipoda of Oregon. Oregon State Monographs, Studies in Zoology, 8: 103 pp.

_____ **1959.** Estuarine Amphipoda. *In*: Ecology of Amphipoda and Polychaeta of Newport Bay, California by J.L. Barnard and D.J. Reish. Allan Hancock Foundation Publications Occasional Paper, 21: 13–69.

_____ **1962.** Benthic marine Amphipoda of southern California: Families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae. Pacific Naturalist, 3: 1–72.

_____ **1964.** Marine Amphipoda of Bahia de San Quintin, Baja California. Pacific Naturalist, 4(3): 55–139.

_____ **1966.** Submarine canyons of southern California. Part V. Systematics: Amphipoda. Allan Hancock Pacific Expeditions, 27(5), 166 pp.

_____ **1967.** Bathyal and abyssal gammaridean Amphipoda of Cedros Trench, Baja California. U.S. National Museum Bulletin, 260. 206 pp.

_____ **1969a.** The families and genera of marine gammaridean Amphipoda. U.S. National Museum Bulletin, 271. 535 pp.

_____ **1969b.** Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. U.S. National Museum Bulletin, 258. 230 pp.

_____ **1970.** Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. Smithsonian Contributions to Zoology, 34, 286 pp.

_____ **1971.** Gammaridean Amphipoda from a deep sea transect off Oregon. Smithsonian Contributions to Zoology, 61, 86 pp.

_____ **1973.** Revision of Corophiidae and related families (Amphipoda). Smithsonian Contributions to Zoology, 151, 27 pp.

Bate, C.S. 1856. On the British Edriophthalma. Report of the 25th Meeting of the British Association for the Advancement of Science, 18–62, pls. 12–22.

_____ **1857.** British Amphipoda. Annals and Magazine of Natural History, 19(2): 135–152.

_____ **1862.** Catalogue of the specimens of amphipodous Crustacea in the collection of the British Museum, London. 8 vols.

Bate, C.S. and J.O. Westwood. 1863, 1868. A history of British sessile-eyed Crustacea. London: John Van Voorst, in 2 vols. [1861–1868].

Boeck, A. 1861. Bemaerkninger angaaende de ved de norske Kyster forekommende Amphipoder. Skandinaviska Naturforskare Forhandlingar, 8: 631–677

_____ **1871.** Crustacea Amphipoda borealia et arctica. [separate from:] Forhandlingar i Videnskabs-Selskabet i Christiania: 83–279.

_____ **1876.** De skandinaviske og arktiske Amphipoder. Christiania. 712 pp.

Bousfield, E.L. 1958. Notes on the amphipod genus *Orchestoidea* on the Pacific coast of North America. Bulletin of the Southern California Academy of Sciences, 56(3): 119–129.

_____ **1963.** Investigations on sea-shore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station list. National Museum of Canada Bulletin, 185: 72–89.

_____ **1968.** Studies on littoral marine invertebrates of the Pacific coast of Canada, 1964. I. Station list. National Museum of Canada Bulletin, 223: 49–57.

_____ **1973.** Shallow water gammaridean Amphipoda of New England. Ithica, N.Y.: Cornell University Press, 312 pp.

_____ **1977.** A new look at the systematics of gammaroidean amphipods of the world. Crustaceana, Suppl. 4: 282–316.

_____ **1979a.** The amphipod superfamily Gammaroidea in the northeastern Pacific region: Systematics and distributional ecology. Bulletin of the Biological Society of Washington, 3: 297–357.

_____ **1979b.** A revised classification and phylogeny of amphipod crustaceans. Transactions of the Royal Society of Canada, 16(4): 343–390.

_____ **1982a.** Amphipoda. Gammaridea. Ingolfiellidea. *In*: Synopsis and classification of living organisms. S.P. Parker, ed. McGraw-Hill, New York. Vol. II, pp. 253–285, 293–294.

_____ **1982b.** The amphipod superfamily Talitroidea in the northeastern Pacific region: I. Family Talitridae. Systematics and distribution ecology. National Museum of Natural Sciences (Ottawa). Publications in Biological Oceanography, 11: 1–73.

_____ **1983.** An updated phylogenetic classification and paleohistory of the Amphipoda. Crustacean Issues 1: Crustacean Phylogeny. ed. F.R. Schram. Balkema, Rotterdam. pp. 257–278.

Bousfield, E.L. and N.E. Jarvett. 1981. Station lists of marine biological expeditions of the National Museum of Natural Sciences in the North American Pacific coastal region, 1966 to 1980. Syllogeus 34: 66 pp.

Bousfield, E.L. and D.E. McAllister. 1962. Station list of the National Museum marine biological expedition to southeastern Alaska and Prince William Sound. National Museum of Canada Bulletin, 183: 76–103.

Bousfield, E.L. and N.L. Tzvetkova. 1982. Studies on Dogielinotidae (Amphipoda: Gammaridea) of the North Pacific region. *In*: Invertebrates of Coastal Biocoenoses of the Arctic Ocean and of the Pacific Ocean. Explorations of the Faunas of the Seas of the USSR, 29 (37): 76–95. 6 figs.

Brüggen, E. v.d. 1905. Die Amphipoden des Katharinenhafens (Murmanküste) und seiner Umgebungen. St. Pétersbourg, Travaux société impériale des naturalistes, 36 (1, 8): 1–10.

_____ **1907.** Zoologische ergebnisse der russischen expeditionen nach Spitzbergen. St. Pétersbourg, Académie impériale des sciences, Musée Zoologique. Annuaire, 12: 214–245.

_____ **1909.** Beiträge zur Kenntnis der Amphipoden-fauna der russischen Arctis. St. Pétersbourg, Académie impériale des sciences. Memoires, ser. 8, vol. 18, 11 (1906), pp. 214–245, figs. 1–9.

Bruzelius, R.M. 1859. Bidrag till kännedomen om Skandinaviens Amphipoda Gammaridea. Stockholm, Konigla Svenska Vetenskaps Akademiens Handlingar, 3: 1–104.

Bulycheva, A.I. 1951. New species of Amphipoda of the Barents Sea. Comptes-rendus de l'Académie des sciences de l'URSS, n.s. 77: 925–928. (In Russian).

_____ **1952.** New species of Gammaridae from Japan sea. Travaux de l'Institut zoologique de l'Académie des Sciences de l'URSS, 12: 194–250. (In Russian).

Chevreux, E. and L. Fage, 1925. Amphipodes. Faune de France 9: 1–488.

Chilton, C. 1884. Additions to the sessile-eyed Crustacea of New Zealand. Transactions and Proceedings. Royal Society of New Zealand, 16: 249–265.

Coulan, K.E. 1982. Revision of the gammaridean amphipod family Ampithoidae using numerical analytical methods. Canadian Journal of Zoology, 60(8): 2015–2027.

Coulan, K.E. and E.L. Bousfield, 1982a. The amphipod superfamily Corophiodea in the northeastern Pacific region: 1. Family Ampithoidae. Systematics and distributional ecology. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography, 10(2): 41–75.

_____ **1982b.** The amphipod superfamily Corophioidea in the northeastern Pacific region: 2. Family Aoridae. Systematics and distributional ecology. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography, 10(3): 77–101.

Dana, J.D. 1853. Crustacea, Part II. U.S. Exploration Expedition 14: 689–1618.

Della Valle, A. 1893. Gammarini del Golfo di Napoli. Fauna und Flora des Golfes von Neapel 20: 948 pp.

Dickinson, J.J. 1982. The amphipod family Ampeliscidae in the northeastern Pacific region: 1. Genus *Ampelisca*. Systematics and distributional ecology. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography, 10(1): 1–39.

_____ **1983.** The amphipod family Ampeliscidae in the northeastern Pacific region: 2. Genera *Byblis* and *Haploops*. National Museum of Natural Sciences (Ottawa) Publications in Natural Sciences, 1: i-vi, 1-38.

Gurjanova, E. 1938. Amphipods, Gammaroidea of Siakhu Bay and Sudzukhe Bay (Japan Sea). Pt. 1. Reports of the Japan Sea Hydrobiological Expedition of the Zoological Institute of the Academy of Science of the USSR in 1934: 241–404 (In Russian).

_____ **1951.** Amphipoda-Gammaridea of the seas of the USSR and adjoining waters. Keys to the Fauna of the USSR. Zoological Institute of the Academy of Science of the USSR, 1029 pp. (In Russian).

_____ **1955.** New species of Amphipoda, Gammaridea from the northern part of the Pacific. Zoologicheskii Institut Akademiia 18: 166–218 (In Russian).

Hansen, H.J. 1887. Malacostraca marina Groenlandiae, occidentalis. Oversigt over det vestlige Grønlands fauna af malakostrake havkrebsdyr: Kjøbenhaven Videnskabelige Meddelelser, 5–226.

Hewatt, W.G. 1946. Marine ecological studies on Santa Cruz Island, California. Ecological Monographs, 16(3): 185–208, figs. 1–2.

Holmes, S.J. 1904. On some new or imperfectly known species of West American Crustacea. Proceedings of the California Academy of Sciences, series 3 (Zool), 3(12): 307–328.

_____ **1908.** The Amphipoda collected by the U.S. Bureau of Fisheries steamer, "Albatross", off the west coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species. Proceedings of the U.S. National Museum, 35: 489–543.

Jarrett, N.E. and E.L. Bousfield. 1982. The amphipod family Lysianassidae in the northeastern Pacific region. 1. Genus *Hippomedon*. Systematics and distributional ecology. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography, 10(4): 103–128.

Johnston, G. 1828. Contributions to the British fauna. Zoological Journal, 3: 175–181.

Krøyer, H. 1842. Nye nordiske slægter og arter af Amfipodernes orden, henhørende til familien *Gammarina*. Krøyer Naturhistorisk Tidsskrift, 4: 141–166.

Kudryashov, V.A. and N.L. Tzvetkova. 1975. New and rare species of Amphipoda (Gammaridea) from the coastal waters of the South Sakhalin. Zoologicheskii Zhurnal, 54 (9): 1306–1315. (In Russian).

Laubitz, D.R. 1977. A revision of the genera *Dulichia* Krøyer and *Paradulichia* Boeck (Amphipoda, Podoceridae). Canadian Journal of Zoology, 55 (6): 942–982.

Liljeborg, V. 1853. Hafs-Crustaceer vid Kullabergi. Skåne. Stockholm Ofversigt af Kongl. Vetenskaps Akademiens Forhandlingar, 9 (1852): 1–13.

_____ **1855.** Ofversigt af de inom Skandinavien hittills fauna arterna af slägtet *Gammarus* Fabr. Stockholm, Kongl. Svenska Vetenskaps Akademiens Handlingar, (1853): pp. 444–460.

Lincoln, R.J. 1979. British marine amphipoda: Gammaridea. British Museum (Natural History), London. 657 pp.

Margulis, R.J. 1963. Additions to the Amphipoda Gammaridea of the Sea of Okhotsk. Crustaceana 5(3): 161–175.

Marschall, A.F.G. 1873. *In* Stebbing, T.R.R. 1906. Amphipoda I: Gammaridea. Das Tierreich, Vol. 21. Verlag von Friedländer und Sohn, Berlin, 806 pp.

McIntosh, W.C. 1874. On the invertebrate marine fauna and fishes of St. Andrew's. Annals and Magazine of Natural History, 14: 258–274.

Mills, E.L. 1961. Amphipod crustaceans of the Pacific coast of Canada. I. Family Atylidae. National Museum of Canada Bulletin, 172: 13–33.

_____ **1962.** Amphipod crustaceans of the Pacific coast of Canada. II. Family Oedicerotidae. National Museum of Canada Natural History Paper 15, 21 pp.

Myers, A.A. 1981. Amphipod Crustacea 1. Family Aoridae. Memoirs of the Hourglass Cruise 5(5): 1–70.

Nagata, K. 1961. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. Publications of Seto Marine Biological Laboratory, 8 (1): 163–182.

Norman, A.M. 1869. Shetland final dredging report, Part II: On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera. Report of the 38th Meeting of the British Association for the Advancement of Science for 1868. 247–336.

Pearse, A.S. 1912. Notes on certain amphipods from the Gulf of Mexico, with descriptions of new genera and new species. Proceedings of the U.S. National Museum, 43: 369–379.

Sars, G.O. 1885. Zoology: Crustacea, I. Norwegian North-Atlantic Expedition 1876–1878, 6: 280 pp.

_____ **1894.** An account of the Crustacea of Norway, with short descriptions and figures of all the species. Parts 22–30. Christiania. 473–671.

Schellenberg, A. 1942. Krebstiere oder Crustacea; IV, Flohkrebse oder Amphipoden. Die Tierwelt Deutschlands. Jenna 40: 1–252.

Shoemaker, C.R. 1916. Descriptions of three new species of amphipods from southern California. Proceedings of the Biological Society of Washington, 29: 157–160.

_____ **1925.** The Amphipoda collected by the United States fisheries steamer 'Albatross' in 1911, chiefly in the Gulf of California. American Museum of Natural History Bulletin, 52: 21–61.

_____ **1931.** A new species of amphipod crustacean (Acanthonotozomatidae) from California, and notes on *Eurysthenes tenuicornis*. Proceedings of the U.S. National Museum, 78 (18): 1–8.

_____ **1941.** A new genus and a new species of Amphipoda from the Pacific Coast of North America. Proceedings of the Biological Society of Washington, 54: 183–185.

_____ **1942.** Amphipod crustaceans collected on the Presidential cruise of 1938. Smithsonian Miscellaneous Collections, 101(11): 1–52.

_____ **1955.** Amphipoda collected at the Arctic Laboratory, Office of Naval Research, Point Barrow, Alaska, by G.E. MacGinitie. Smithsonian Miscellaneous Collections, 128(1): 1–78.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy, the principles and practice of numerical classification. San Francisco: W.H. Freeman. 573 pp.

Staude, C.P., J.W. Armstrong, R.M. Thorn and K.K. Chew. 1976. An illustrated key to the intertidal gammaridean Amphipoda of Central Puget Sound. College of Fisheries, University of Washington, Washington, U.S.A. 24 pp.

Stebbing, T.R.R. 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–76. Report on the Scientific Results of the Exploring Voyage of H.M.S. Challenger: Zoology, 29: 1737 pp. (in 3 parts).

_____ **1906.** Amphipoda 1: Gammaridea. Das Tierreich, vol. 21. Verlag von Friedländer und Sohn, Berlin. 806 pp.

Stephensen, K. 1944. Some Japanese amphipods. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, 108: 25–88.

_____ **1944b.** Amphipoda. Zoology of East Greenland. Meddelelser on Grønland, 121(14): 1–165, fig. 1–18.

Stout, V.R. 1913. Studies in Laguna Amphipoda. Zoologische Jahrbucher Abteilungfür Systematik Oekologie und Geographie der Tiere, 34: 633–659.

Tzvetkova, N.L. 1977. A new genus and new species of amphipods (Amphipoda, Corophioidea) from the Sea of Japan. *In*: New species and genera of Marine Invertebrates. Zoological Institute of the USSR Academy of Sciences, 88–101. (In Russian).

Walker, A.O. 1898. Crustacea collected by W.A. Herdman, F.R.S., in Puget Sound, Pacific coast of North America. Transactions of the Liverpool Biological Society, 12: 268–287.

Walker, A.O. 1904. Report on the Amphipoda collected by Prof. Herdman at Ceylon in 1902. *In*: Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar. Royal Society of London, 1: 229 + 300.

Walker, A.O. 1909. Amphipoda Gammaridea from the Indian Ocean, British East Africa, and the Red Sea. Linnean Society of London Transactions, ser. 2, Zoology, 12 (4): 323–344.

Table 1 Geographic Distribution of Isaeidae Collected from Alaska to Northern California

Genus	Species	Bering Sea & Aleutian Is., Alaska	Prince William Sound, Alaska	Cross Sound to Dixon Entrance, Alaska	Northern B.C. and Queen Charlotte Is., B.C.	Central B.C. and Vancouver Is., B.C.	Wash.	Ore.	Calif.	Other Records
Gammaropsis	*ellisi*	0	0	X	X	X	0	0	0	
	thompsoni	0	0	X	X	X	X	0	X	
	spinosa	0	0	0	0	X	0	0	X	
	shoemakeri	0	0	0	0	X	X	0	0	
Paraeurystheus	*dentatus*	X	0	0	0	0	0	0	0	
	tzvetkovae	X	0	0	0	0	0	0	0	
Podoceropsis	*amchitkensis*	X	0	0	0	0	0	0	0	
	setosa	X	0	0	0	0	0	0	0	
	chionoecetophila	X	0	0	0	0	0	X	0	
	angustimana	0	0	0	0	X	0	0	0	
	barnardi	0	0	0	0	X	0	0	0	a
Photis	*fischmanni*	X	0	0	0	0	0	0	0	a
	cf. *spasskii*	X	X	X	X	0	0	0	0	a
	oligochaeta	0	0	X	X	X	0	0	0	
	pachydactyla	0	0	X	X	X	0	0	0	
	brevipes	0	X	X	X	X	X	X	X	
	bifurcata	0	0	X	X	X	X	X	X	
	macinerneyi	0	0	0	X	X	X	0	0	
	parvidons	0	0	0	X	X	X	0	0	
	lacia	0	0	0	X	X	0	0	X	
	conchicola	0	0	0	0	0	X	0	X	
Protomedeia	*fasciata*	X	0	0	0	0	0	0	0	b
	stephenseni	X	0	0	0	0	0	0	0	c
	grandimana	X	X	X	X	X	0	0	0	d
	prudens	0	0	0	X	X	0	X	X	
	articulata	X	0	0	0	0	0	X	X	a, b
Cheirimedeia	*macrodactyla*	X	0	0	0	0	0	0	0	
	similicarpa	X	0	0	0	X	0	0	0	
	macrocarpa americana	0	0	0	X	X	X	X	0	
	zotea	0	0	0	0	X	X	0	X	
Chevalia	*aviculae*	0	0	0	0	X	0	0	X	e
Number of Species		13	3	8	13	19	9	6	10	
% of Species in Common with Next District			14	38	62	60	40	33	33	

X = present
0 = absent

[a] U.S.S.R.
[b] Sea of Okhotsk, Arctic Ocean, North Atlantic, North Sea
[c] Iceland, Norway, Greenland
[d] Sea of Okhotsk, Murman Coast? Kara Sea? Spitzbergen
[e] Tropicopolitan: Indian Ocean, South Africa, Caribbean Sea, eastern Pacific Ocean

Table 2 Exposure, Salinity and Depth Range of Isaeidae Collected from Alaska to Northern California

Genus	Species	COASTAL EXPOSURE		SALINITY RANGE			DEPTH RANGE		
		Open and Semi-Protected	Protected	Marine Polyhaline (28‰)	Meso-Haline (10–27‰)	Oligohaline and Fresh Water (9‰)	Subtidal Max. Depth Record (m)	Low-Water to Mean-Water	Mean-Water to High Water
Gammaropsis	*ellisi*	X	0	X	0	0	72	X	0
	thompsoni	X	0	X	0	0	72	X	0
	spinosa	X	0	X	0	0	27	X	0
	shoemakeri	X	0	X	0	0	27	X	0
Paraeurystheus	*dentatus*	X	0	X	0	0	90	0	0
	tzvetkovae	X	0	X	0	0	—	—	—
Podoceropsis	*amchitkensis*	X	0	X	0	0	0	X	0
	setosa	X	0	X	0	0	0	X	0
	chionoecetophila	X	0	X	0	0	600	0	0
	angustimana	X	0	X	0	0	72	0	0
	barnardi	X	0	X	0	0	17	X	0
Photis	*fischmanni*	X	0	X	0	0	38	0	0
	cf. *spasskii*	X	0	X	X	0	21	X	0
	oligochaeta	0	X	X	0	0	22	X	0
	pachydactyla	X	0	X	0	0	90	X	0
	brevipes	X	X	X	X	0	108	X	0
	bifurcata	X	0	X	X	0	60	X	0
	macinerneyi	X	X	X	0	0	45	X	0
	parvidons	X	X	X	X	0	54	X	0
	lacia	X	0	X	0	0	40	0	0
	conchicola	X	0	X	0	0	0	X	0
Protomedeia	*fasciata*	X	0	X	0	0	150	0	0
	stephenseni	X	0	X	0	0	30	0	0
	grandimana	X	0	X	X	0	200	X	0
	prudens	X	0	X	X	0	400	X	0
	articulata	X	0	X	0	0	906	0	0
Cheirimedeia	*macrodactyla*	X	0	X	0	0	30	0	0
	similicarpa	X	X	X	0	0	67	0	0
	macrocarpa americana	X	X	X	X	0	0	X	0
	zotea	X	0	X	X	0	113	X	0
Chevalia	*aviculae*	X	0	X	0	0	8	X	0
Number of Species		28	6	29	8	0	26	19	0

X = present
0 = absent
— no data available

Table 3 Comparison of Generic Level Characters Utilized in Cluster Analysis of the Regional* Isaeidae (Fig. 33). Plesiomorphic Values Are Coded "0", Apomorphic Values Are Coded "1"

Character	Apomorphic State	Proportion of regional* species possessing the apomorphic character							
		Photis	*Protomedeia*	*Cheirimedeia*	*Gammaropsis* (northern group)	*Gammaropsis* (southern group)	*Paraeurystheus*	*Podoceropsis*	*Chevalia*
Body	Peraeon 6–7 and pleon greatly enlarged	0	0	0	0	0	0	0	1
	Plates 1–3 acutely produced posterodistally	0	0	0	0	0	0	0	1
	Strongly laterally compressed	0	0	0	0	0	0	0	1
	Dorsoventrally depressed	0	1	1	0	0	0	0	1
	Bearing dorsal setae	0	1	1	1	.3	1	8	1
	Lacking dorsal cusps	1	1	1	0	.8	0	1	1
	Urosomites 1 and 2 fused	0	0	0	0	0	0	0	1
Coxae	Progressively shallowing posteriorly	0	1	1	0	0	0	0	1
	Not contiguous	0	0	0	0	0	0	0	1
	Deeper than wide	1	0	0	.6	.5	.3	.1	0
	Bearing long marginal setae	.8	1	1	0	0	.2	.2	0
	Coxa 1 anteriorly produced	.2	1	1	0	.1	1	0	1
Head lobe	Acute	1	0	0	.8	.6	.1	1	0
Eye	Round, oval or lenticular	1	1	1	.3	.8	.8	1	1
	Small	1	.9	1	.3	.3	.6	.5	1
Antenna 1	Peduncular seg. 3 > ¾ seg. 1	.8	0	0	1	1	0	1	1
	Accessory flagellum minute	1	0	0	0	0	0	1	0
Antennae 1 and 2	Flagellae subequal	.9	1	1	0	.3	0	.9	0
	Flagellum 2 ≤ peduncular segment 5	.2	1	1	0	.3	.8	.2	0
Upper lip	Epistome acutely produced	.5	0	0	1	.5	0	.9	0
Mandible	≥ 5 raker spines	0	0	0	1	0	0	.8	0
	Palp, segment 3 not distally broadened	.8	1	1	0	0	0	0	1
Maxilla 1	Inner plate not setose	1	0	0	0	1	0	0	0
Maxilla 2	Facial setae absent	.1	1	1	0	0	0	0	0
Gnathopod 1	Segment 5 post. lobe < ¾ ant. margin	.6	0	0	0	0	0	0	0
	Palm transverse or simple	0	.9	.8	0	0	0	1	1
	Dactyl strongly overlapping palm	0	1	.8	0	0	0	1	1

Character	Apomorphic State	Proportion of regional* species possessing the apomorphic character							
		Photis	*Protomedeia*	*Cheirimedeia*	*Gammaropsis* (northern group)	*Gammaropsis* (southern group)	*Paraeurystheus*	*Podoceropsis*	*Chevalia*
Gnathopod 2	Segment 2 bearing stridulation ridges (♂)	1	0	0	0	0	0	0	0
	Segment 5 ≤ ½ segment 6 (♂)	1	0	0	.3	.3	1	1	0
	Segment 5 posteriorly lobed (♂)	1	0	0	0	.3	.8	0	1
	Palm strongly incised (♂)	.9	0	0	.1	0	0	0	0
	Dactyl altered in shape (♂)	.4	.2	0	0	0	0	.1	0
Peraeopod 3	Segment 4 anteriorly strongly setose	1	1	0	0	0	0	0	0
	Segment 4 anterodistally produced over segment 5	1	0	1	0	.3	0	1	0
	Segment 5 ≤ ⅓ segment 4	.9	.7	.9	0	.8	0	1	1
Peraeopods 3 and 4	Dactyls very long	0	1	1	0	0	0	0	0
Peraeopod 5	Much reduced	0	0	0	0	0	0	0	1
	Segment 2 posterodistal corner notched (♂)	0	0	0	0	0	0	1	0
	Dactyl bearing an accessory tooth	1	0	0	0	0	0	0	1
Peraeopods 5–7	Segment 2, hind margin bearing plumose setae	.1	1	1	0	0	0	.2	0
	Segment 5 bearing comb spines	0	1	.8	1	.6	.2	.8	0
Brood plates	Narrow	0	1	1	0	0	0	0	1
	Setae hook-tipped	0	0	0	1	1	1	1	0
Epimera 1–3	Not posteriorly notched	1	1	1	0	.6	.2	1	1
	Lateral ridge absent	1	.8	1	0	.6	0	1	1
Uropod 1	Peduncular spinous process absent	1	0	0	0	0	0	0	0
Uropods 1 and 2	Rami terminate in a single spine	1	0	0	0	0	0	0	0
Uropod 3	Outer ramus terminally setose	1	.2	.7	0	.3	1	1	1
	Outer ramus bisegmented	1	0	0	0	0	0	0	0
	Inner ramus ≤ ½ outer ramus	1	.1	.6	0	0	.2	0	0
Telson	Longer than broad	.6	.3	.1	0	.3	0	0	1
	Bearing spines (other than usual cusps)	0	0	0	1	0	0	0	0
Total		27.8	22.1	22.7	9.4	11.6	9.2	20.5	24.0
% Apomorphy		53.5	42.5	43.7	18.1	22.3	17.7	39.4	46.2

* All North Pacific species analysed in Figs. 34–36

POOR

QUALITY

ORIGINAL